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Effects of Wolf Predation on Recruitment of Black-tailed Deer on Northeastern Vancouver Island

by I.W. Hatter
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by

Ian W. Hatter

Wildlife Branch
Ministry of Environment
Victoria, B.C.

Wildlife Report No. R-23
June 1988

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ABSTRACT

Columbian black-tailed deer (*Odocoileus hemionus columbianus* Richardson) populations on northern Vancouver Island showed marked declines during the 1970's, coincident with a major increase in numbers of the Vancouver Island wolf (*Canis lupus crassodon* Hall). Reduced recruitment appeared to be the major cause for the deer declines. The objective of this study was to test the hypothesis that wolf predation was the primary factor limiting recruitment A study area, located within a moderate wolf density region on the Island, was selected for intensive study from 1980-82.

Examination of reproductive tracts from 20 female deer collected during the last trimester of pregnancy indicated that fetal growth and fetal rates were comparable to other deer populations on the Island prior to the increase in wolves. The physical condition of 28 deer in spring, based on a kidney fat index and a condition index, indicated pregnant does and fawns were in fair to good condition. Age-specific eviscerated body weights from 69 harvested female deer in the study area were comparable to annual mean female deer weights from 1957-64 on northern Vancouver Island.

The extent, timing, and causes of fawn mortality were documented from 26 radio-tagged neonates and from deer herd composition counts. Mortality rates from radio-tagged fawns were similar to non-tagged fawns. Fawn mortality by the end of August was estimated at 63% with most of the mortality occurring in June and July. Summer fawn mortality appeared to be greater in 1981 than in 1980, but this appears to have been partially confounded by sampling biases. Of 14 fawns that died, eight were attributed to wolf predation, one to bear predation, two to accidents, one to disease, one to malnutrition, and one to hunting. Scat analysis indicated juvenile cervids, primarily fawns, composed the bulk of the wolves' summer diet. Monthly fawn survival was inversely related to the percent occurrence of fawns in wolf scats. Although bear and cougar predation was probably additive to wolf predation, they were not considered to be significant predators on fawns. Hunting, through increased selection for fawns as the deer herd declined, may have also been an additive factor to wolf predation. Accidents, disease, parasites, and malnutrition also did not appear to be limiting recruitment.

The average natal (June-August) home range for nine fawns with 10 or more radio-locations was 23 ha. Movements tended to be greater in August as fawns became more active. Of 237 fawn relocations in 1981, 86% were in cutover habitats. Telemetry of two fawns throughout their first year, as well as monthly night counts in spring and summer, suggested that deer in the study area were resident rather than migratory.

Pack territories for two wolf packs were determined from 454 locations of four radio-tagged wolves. Although wolf densities in the Adam River watershed probably only declined slightly since 1978, intrapack densities of the two studied packs declined by 60%. This resulted from territorial expansion of both packs during 1981 and possibly 1980.

The small natal home ranges of deer fawns and the resident behaviour of the deer herd allowed an opportunity to examine fawn survival and recruitment relative to wolf pack home ranges and summer home sites. Survival of radio-tagged fawns was highest on the edge of home ranges where wolf activity was less intensive

and lowest near homesites. August fawn:doe ratios and spring carryover were lowest in areas used most frequently by wolves.

It was concluded that wolf predation is presently the primary factor limiting deer recruitment on northern Vancouver Island. A reverse sigmoid growth curve in deer population trends with continuing depressed recruitment, and supporting evidence of low equilibria developing in other coastal wolf- deer systems, suggest that without a marked artificial reduction in wolf numbers, wolves will continue to maintain low deer numbers for several more years. Although a protracted deer recovery, following a natural reduction in wolf numbers is anticipated, the lengthy period probably required to produce a major increase in deer numbers indicates that it is not compatible with deer management objectives. It is therefore recommended that wolf control, in combination with restricted harvest, be initiated to increase deer populations and to maintain a more viable wolf-deer system on the Island.

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1. INTRODUCTION

1.1. Background

Black-tailed deer on Vancouver Island are one of the most popular big game species in British Columbia. From 1964-1974, the deer harvest on the Island averaged 23 000 deer annually and contributed 30 - 45% of the total deer harvest in the province (Hebert 1979). In 1976, northern Vancouver Island (Management Units (M.U.'s) 9-13) supported 29% of the provincial harvest and 10% of the provincial deer hunter days. Estimated annual revenues generated from harvests on the Island exceeded 2 million dollars in 1977 (B.C. Fish and Wildlife Branch, unpubl.).

Traditionally, deer research on Vancouver Island has had a strong habitat-related basis (Smith 1968; Edie and Harestad 1971; Wilms 1971; Smith and Davies 1973; Jones 1975; Stevenson 1978; Bunnell 1979; Harestad 1979; Rochelle 1980; Harestad *et al.* 1982) with management focused on the preservation of critical old-growth winter ranges and regulating the hunter harvest (Hebert 1979). During the early 1970's, a major increase in wolf numbers occurred throughout northern Vancouver Island (Hebert *et al.* 1982; Jones and Mason 1983). Subsequent declines in deer numbers and in the hunter harvest led to a concern over the effects of wolf predation on deer and to the ability to meet deer management objectives (Hebert 1981). Deer night counts from 1976-80 indicated populations in specific watersheds declined at an annual rate of 19% where wolf densities were high, 4-9% where densities were moderate, and increased at 29-34% where densities were low (Fig. 1, B.C. Fish and Wildlife Branch, unpubl.). These declines appeared to be related to reduced fawn survival since field classifications indicated spring carryover (% fawns at 10 months of age of total deer observed) was similarly related to wolf densities, averaging 10% in the high wolf density areas, 25% in the moderate density areas and 31% in the low density areas. Associated information indicated summer fawn:doe ratios were also low in the moderate and high wolf density areas, suggesting heavy mortality of fawns during their initial 3 months of life (B.C. Fish and Wildlife Branch, unpubl.; Jones and Mason 1983). Weather, habitat, other predators, and hunting were not believed to be sufficient causes to account for the declines, although each of these factors received limited investigation.

Preliminary wolf investigations on northern Vancouver Island suggested one of the highest wolf densities in North America (e.g. Adam River 1978: 1 wolf/17 km^2 in entire watershed, 1 wolf/ 6 km^2 in the Upper Adam) (Scott 1979; Hebert *et al.* 1982). Scott and Shackleton (1980) indicated that black-tailed deer were the major year-round prey item of wolves with fawns comprising a substantial portion of the summer diet.

Many predator-prey studies have considered wolf predation to be of either minor importance in controlling prey populations (Cowan 1947; Thompson 1952; Carbyn 1974, 1980) or else identified severe weather and/or declining habitat quality which predisposed ungulates to intensive wolf predation (Mech and Karns 1977; Peterson 1977). In other cases, human harvests on the prey species in combination with predation have been linked to prey declines (Haber 1977; Haber and Walters 1980). Gasaway *et al.* (1983) noted that moose (*Alces alces*) declines in interior Alaska were related to a combination of severe winters, hunting, and wolf predation. Bergerud (1980,1983) and Bergerud *et al.* (1983), however, considered wolf predation to be capable of limiting some caribou and moose populations in the absence of other environmental influences.

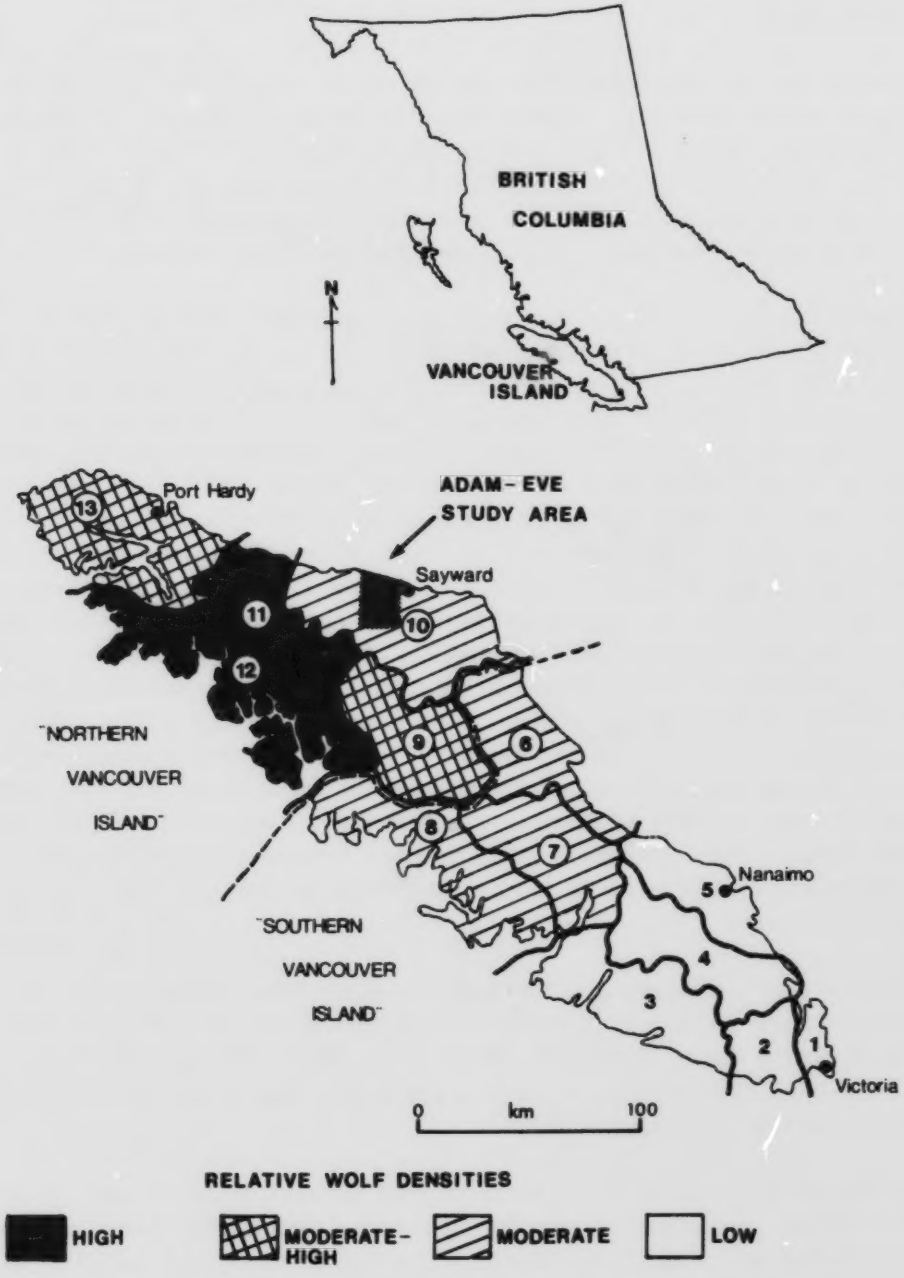

Figure 1. Wolf regions on Vancouver Island, 1976-79. Wildlife management units (M.U.'s) are also shown. M.U.'s 1 to 8 are referred to as southern Vancouver Island and M.U.'s 9-13 as northern Vancouver Island. Relative wolf densities are based on univariate cluster analysis of the wolf hunter sighting index (Hebert *et al.* 1982).

The dissimilarity in findings from these studies, as well as a lack of research on wolf-ungulate relationships in coastal forestry ecosystems, indicated that a closer examination of wolf predation on northern Vancouver Island was required. The intent of this study was to increase understanding of wolf-deer relationships on the Island and provide information for choosing the appropriate option to managing this wolf - ungulate - coastal forest system.

1.2. Scope and Objectives

Birth, death, immigration, and emigration are the four fundamental demographic parameters in any study of population dynamics. Assuming immigration and emigration are negligible or counter-balanced, the analysis of an ungulate population trend can be based on three reductions in the population each year: (a) a decrease in natality, (b) mortality of juveniles (e.g. under 1 year of age) and, (c) mortality of adults (Sinclair 1973). Since summer fawn:doe ratios and spring carryover on northern Vancouver Island showed marked reductions, it was apparent that the major processes operating in the deer declines were either a, b or both a and b. As recruitment, which is defined as the addition of juveniles into a population at some significant time after birth, integrates both natality and juvenile mortality, the effects of wolf predation on various deer recruitment rates (August fawns: 100 does, % spring carryovers) were chosen to bound the investigation.

Numerous factors interact to affect recruitment (Fig. 2). A complete examination of wolf predation on recruitment must consider these factors as well as their interrelationships For example, logging alters forest succession, thereby influencing habitat quality and quantity. Poor habitat conditions (reduced food and cover), in turn, may independently or in combination with severe winter weather, depress the nutritional status of does and lower productivity (Cheatum and Severinghaus 1950; Taber and Dasmann 1957). Alternatively, does subjected to grave nutritional stress during late pregnancy may maintain high productivity but retard fetal development and give birth to stunted fawns that subsequently die (Verme 1962, 1963, 1965). Although wolves could be the principal cause of death for most of these fawns, the impact of predation on the deer herd would ultimately be due to more basic ecological factors related to weather and/or habitat quality. Hunting, disease, parasites, and accidents remain other potentially important sources of mortality, although increased disease or parasite loads are also likely nutritionally related (Longhurst 1955). Logging may also alter deer hiding or escape cover, which could increase the susceptibility of fawns to predation (Salwasser *et al.* 1978). Wolf travel or hunting routes may be enhanced by forestry practices (e.g. logging roads), thereby reducing search time and increasing the functional response of wolves, resulting in higher kill rates (Bergerud 1981).

This study's objective was to test the hypothesis that wolf predation is the primary factor limiting recruitment, i.e., it outweighs all other factors. Predictions of the hypothesis that were investigated are outlined below as two stages in the hypothesis falsification process: one relation to non-predation causes (Stage I); and one relating to predation (Stage II).

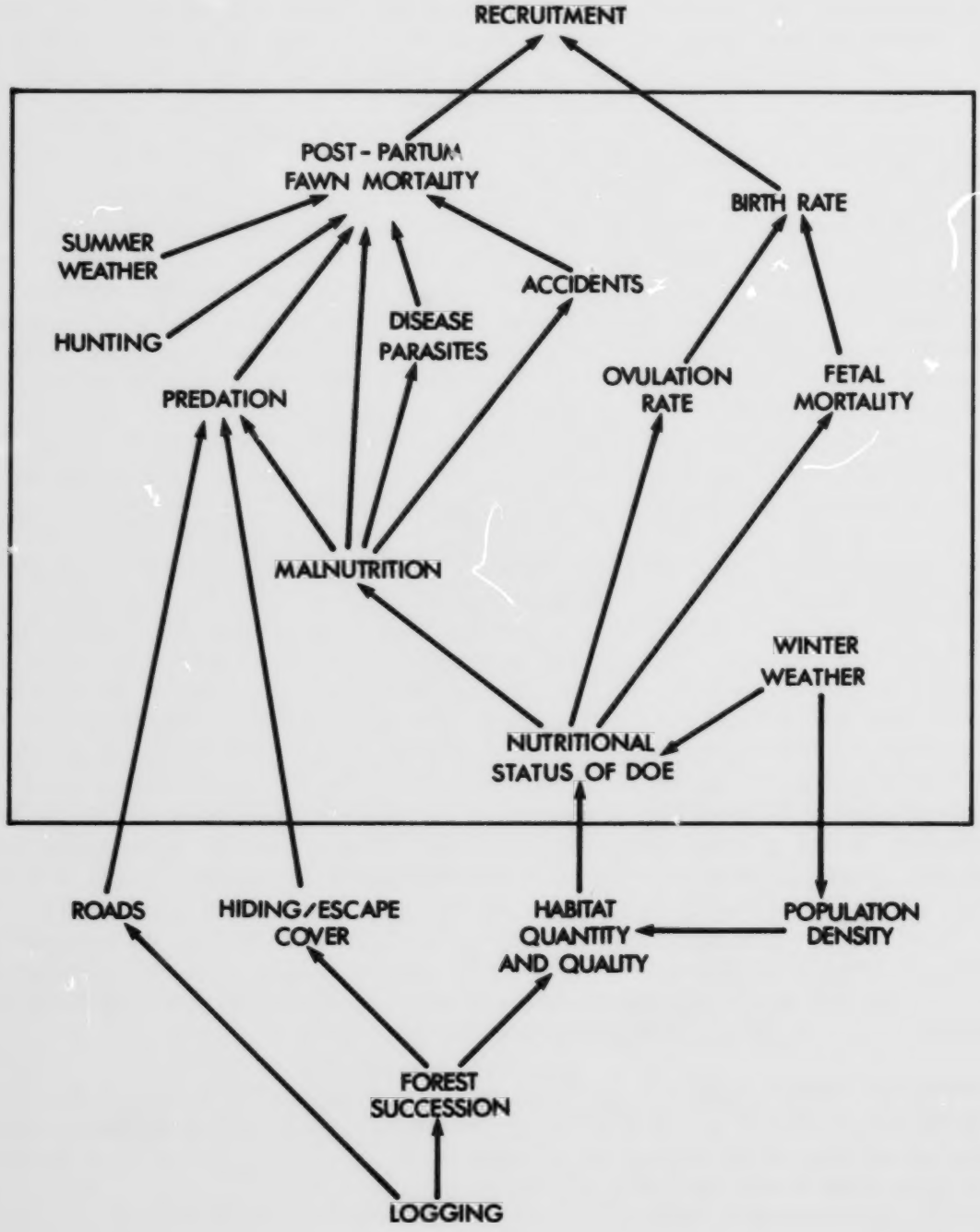

Figure 2. Model illustrating the processes affecting recruitment. Those factors investigated in this study are shown within the box.

Stage I: Non-predation losses are negligible or have remained unchanged since the increase in wolf numbers.

(a) birth processes:

i. fetal growth is normal
ii. birth rates are not depressed
iii. maternal condition of does is adequate to produce viable offspring

(b) death processes:

i. malnutrition in fawns is negligible or unchanged
ii. disease and parasites of fawns are negligible or unchanged
iii. accidents resulting in death of fawns are negligible or unchanged
iv. hunting of fawns is negligible or unchanged.

By way of exclusion, predation remains as the cause of low recruitment.

Stage II: If wolf predation is the principal factor, i.e. it is not possible to evoke alternative causes for low recruitment, then the following predictions should hold:

i. most fawns die from wolves
ii. fawns comprise a major portion of the wolves diet
iii. deaths due to other predators are negligible or unchanged
iv. recruitment rates vary inversely with wolf activity or wolf density.

This study was sponsored by the B.C. Ministry of Environment, Fish and Wildlife Branch, Region 1. Dr. Daryll Hebert, now Regional Wildlife Biologist in Williams Lake, initiated the study, provided direction with the research design, and found the monies necessary to conduct the study. Dr. Ernest Ables, my major professor, provided helpful guidance and suggestions during my stay at the University of Idaho. Drs. Donald Johnson and James Peek, also members of my graduate committee, gave freely of their time in reviewing the manuscript.

Many other individuals contributed to various portions of the study. Ralph Archibald, Rick Davies, Laura Friis, James Hatter, Doug Janz, Herb Langin, Bud Smith, and John Youds contributed extensively to both field and laboratory work. I extend special thanks to Byron Mason for his constant enthusiasm, friendship, and assistance in conducting deer surveys. I also thank Don Eastman, Alton Harestad, and Greg Jones for many enlightening discussions.

The B.C. Ministries of Environment and Forests, the Nanaimo Fish and Game Club, World Wildlife Fund, University of British Columbia, and O & J Enterprises provided financial and logistical support. The B.C. Fish and Wildlife Branch permitted use of their data which helped to make this thesis more complete. A.S. Harrison ably drafted many of the figures.

Finally, and most especially, I thank my wife Linda, who participated in every phase of this project, and supported me in more ways than she realizes.

2. STUDY AREA AND STUDY PERIOD

The study area, referred to as the Adam-Eve, is located within the moderate wolf density region on northeastern Vancouver Island, 15 km west of Sayward, B. C. (Fig. 1). The area, encompassing 530 km^2 of the lower Adam and Eve river valleys, was considered large enough to discount immigration and emigration as significant factors influencing deer population dynamics. Intensive wolf activity was first noted in 1976 (B. Mason, pers. comm.). Since 1978 two wolf packs were known to have resided within the area (Scott 1979; Scott and Shackleton 1982; B.C. Fish and Wildlife Branch, unpubl.). The Adam-Eve was chosen over a site in a high wolf density region due to the existing wolf information and the availability of a relatively dense deer population for sampling. Also annual deer classification and night counts conducted by the British Columbia Fish and Wildlife Branch since 1967 were available, although standardized census procedures were not adopted until 1976.

The majority of the study area occurs within the Coastal Western Hemlock biogeoclimatic zone, although small portions at low elevations lie within the wet subzone of the Coastal Douglas-fir biogeoclimatic zone (*sensu* Krajina 1965). The area is being logged by MacMillan Bloedel Ltd. (TFL's 7 and 39): extensive young second-growth forests occur in the valley bottoms and lower sidehills. A network of logging roads covers the entire area. Highway 19 traverses east to west through the study area. Figure 3 shows mean daily temperature, rainfall, and snowfall recorded at Sayward since 1973.

The large mammal fauna within the study area include black-tailed deer, Roosevelt elk (*Cervus elaphus*), wolves, black bears (*Ursus americanus*), cougars (*Felis concolor*), and beaver (*Castor canadensis*).

Intensive field work began in May 1980 and continued to September 1981. Field work was conducted daily from May to September. Bimonthly trips of 7 to 10 days duration were made during the winter 1980-81. Special trips were made in September and November in 1979, 1980, and 1981 to collect hunter harvest information, and in May 1982 to classify deer herd composition.

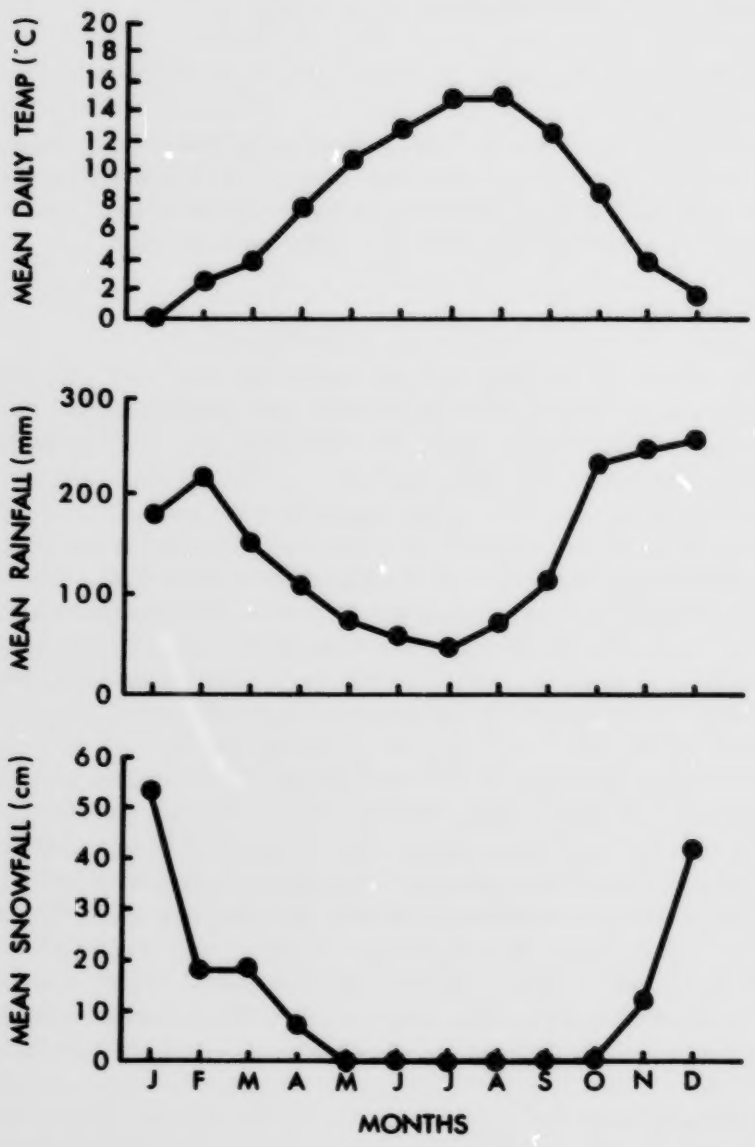

Figure 3. Mean daily temperature, rainfall, and snowfall recorded at Sayward, B.C. based on adjusted normals (1973-80).

3. MATERIALS AND METHODS

3.1. Weather Severity

Cumulative snowfall from November to April at Port Hardy was used to reflect the historical pattern of winter severity for northern Vancouver Island. Snowfall and June rainfall data from Sayward, available since 1973, were considered to be more representative of local conditions in the study area and were used to examine the effects of weather on recruitment.

3.2. Collection of Deer Specimens

Deer were collected in May by shooting, although road-killed deer were also examined. Efforts were made to collect fawns and does. Each specimen was weighed to the nearest pound and external measurements recorded in centimetres. The mandibles, both kidneys, and one femur were removed and frozen. An incisor was later removed from the mandible and sent to the British Columbia Fish and Wildlife Branch Wildlife Research Laboratory for sectioning and aging (Thomas and Bandy 1973). Tissue samples were taken from all major organs. Histological samples were preserved in 10% formaldehyde and samples for pathology were frozen. Tissue samples were later sent to the Clearbrook Veterinary Laboratory (British Columbia Ministry of Agriculture and Food) for examination. The reproductive tract was removed from females and the number and sex of fetuses, forehead-rump length, chest girth, hind foot length, and weight were recorded.

During September and November 1980-81, hunters were requested to have their deer weighed, the chest girth and hind foot length measured, and the lower mandible removed for aging by wear-class. Mandibles were sent to the Wildlife Branch, Nanaimo for aging. Tooth wear analysis to identify age classes beyond 4.5 years is not accurate (Thomas and Bandy 1973). Therefore, older age classes were lumped into a 5.5+ age class. A 9-day hunting season for does and fawns in November was used to estimate the age-class structure of the female population and to determine the ratio of fawns to does in the harvest. Hunter selectivity for fawns (%) was measured as (fawn:doe ratio in hunter game check - August fawn:doe ratio)/ August fawn:doe ratio x 100. Hunters were also asked to submit the lungs from their deer. These were checked for hydatid cysts by Dr. T. Mace, parasitologist, in 1980, and by the Clearbrook Veterinary Laboratory in 1981.

3.3. Physical Condition of Deer

Deer physical condition, as indicated by fat reserves, was assessed from deer collected in May. Kidneys were weighed with and without the attached fat to calculate the kidney fat index (KFI) (Trainer *et al.* 1979):

$$KFI = (\text{kidney fat weight}/\text{kidney weight}) \times 100$$

The femur marrow fat content (FMF) was estimated by measuring the percentage water (H_2O) in a sample of femur marrow as described by Coblentz (1979), and converted to percentage fat by the regression equation developed for black-tailed deer by Coblentz:

$$FMF = 98.37 - 1.23(H_2O)$$

The KFI and FMF were combined to form a condition index (CONINDEX) developed by Trainer *et al.* (1979). This index is reasonably well correlated with the physical condition scoring system developed by Kistner *et al.* (1980). The CONINDEX is expressed as:

$$CONINDEX = (KFI - 20) + FMF \text{ for } KFI \geq 20;$$

or

$$CONINDEX = FMF \text{ for } KFI < 20$$

Deer physical condition, as indicated by eviscerated body weight, was assessed from hunter-harvested deer in the fall.

3.4. Fawn Capture, Monitoring, and Relocation

Neonates (about 1 to 5 days of age) were located in June by glassing cutovers during crepuscular periods, spotlight searches at night, and by driving logging roads during daylight hours. Searching was restricted to the lower Adam River areas as costs of daily monitoring in both the Adam and Eve were considered too prohibitive. All captured fawns were weighed, measured, sexed, and ear tagged with numbered Rototags (Nasco Co.) (Appendix A). Rectal swabs were obtained for most fawns and sent to the Clearbrook Veterinary Laboratory to be cultured for enteric bacteria. Initial attempts to take blood samples from neonates proved difficult, greatly increased handling time, and therefore was abandoned. Each fawn was outfitted with a mortality-sensing radio-transmitter attached to a break-away collar (Telonics Inc.). The radios operated in the 150-151 mHz range and doubled their pulse rate whenever the unit was motionless for 4 hours; a fast pulse theoretically indicated a mortality had occurred. Collars were designed to break off when fawns were approximately 10 months of age.

To determine if the signal was on normal or mortality mode, the radio- tagged fawns were checked with a truck-mounted antenna. Checks were made at least twice daily in June, daily during July and August, and intermittently thereafter (about 10-15 times per month) until the fawn died, radio contact was lost, or the collar fell off. When the mortality unit was activated, a 3-element Yagi antenna was used to locate the suspected kill. Upon reaching the suspected mortality site, a thorough search of the fawn and the surrounding area was made to determine the cause of death. Observations were recorded on a mortality form adapted from Ballard and Taylor (1978) (Appendix B). Criteria used to determine predator-involved mortalities and the predator species were a combination of those used in other fawn mortality studies (Table 1, see Garner *et al.* 1976 for a review). All dead radio-tagged fawns not killed by predators were retrieved and sent to the Clearbrook Veterinary Laboratory for necropsy.

Table 1. Criteria used to determine predator-involved fawn mortalities and predator species

1. Characteristics of wounds or death site	
A. Blood around wounds, in nostrils, ears, throat, and around mouth	predator involved
B. Blood not around wounds, carcass remains show no evidence of bruises or hemorrhaging	predator scavenged
C. Blood on grass in area and/or evidence of struggle by fawn at site	predator involved
D. Fawn observed within 48 hours prior to location of carcass and at that time appeared in good physical condition	predator involved
E. Carcass retrieved within 12-24 hours of death and had been partially or totally consumed	predator involved
F. Carcass lacks signs of being bitten	predator not involved
2. Carcass disposition	
A. Laying in open, no attempt at concealment, carcass remains not scattered	unknown predator
B. Laying in open, no attempt at concealment, remains scattered	unknown predator
C. Carcass partially or completely covered by litter	cougar or black bear
D. Partially or completely buried	cougar, black bear or wolf
3. Carcass consumption	
A. All consumed	unknown predator
B. All consumed except hide and larger leg bones left intact	unknown predator
C. Hide inverted	black bear
4. Predator sign in area	
A. Fresh wolf tracks, scats, or hairs	wolf
B. Fresh cougar tracks, scats, or hairs	cougar
C. Fresh bear tracks, scats, or hairs	black bear

The method of Trent and Rongstad (1974) was used to calculate survival rates (p_x) from radio-telemetry data. Monthly survival is given by:

$$p_x = \left(\frac{x-y}{x} \right)^n$$

where x is the number of radio-fawn days and y is the number of deaths observed over n days (1 month). A radio-fawn day is 1 radio-tagged fawn in the field for 1 day. Assumptions of the method are: (1) each fawn day is an independent trial, and (2) there is a constant probability of survival for each trial over a time period of n days (Trent and Rongstad 1974). Radio-fawn days, rather than the actual number of radio-tagged fawns, was used to estimate mortality because several radio transmitters failed, leaving an incomplete record for some fawns. The use of radio-days eliminates these problems and provides data equivalent to complete records for tagged fawns. Summer (June - August) and summer-fall (June - November) survival was calculated as the product of the monthly survival rates.

Radio-tagged fawns were located on the ground by vehicle using a truck- mounted whip antenna and a hand-held, 3-element Yagi antenna. The date, time of day, animal state (active or inactive radio signal), and compass direction of the radio signal were recorded for each bearing. At least three bearings were taken, and the collar's location estimated by triangulation on 20 chain (1 cm = 158.4 m) maps. The location estimate was judged to be either accurate, rough, or very rough, depending on the degree of intersection of the bearings as described by Harestad (1979). The fawn was considered active if two or more consecutive bearings had active signals (Jackson *et al.* 1972). The habitat type (cutover or forested) occurring within the approximate centre of the error polygon was recorded. Telemetry locations were used to calculate natal (June - August) home ranges by the minimum home range method (Mohr 1947). Due to problems with the radio-telemetry equipment in 1980, little emphasis was placed on delineating home ranges for radio-tagged fawns. In 1981, I attempted to obtain at least 10 radio-locations per fawn each month.

3.5. Deer Herd Composition Counts

Herd or population composition counts were conducted in June, July, August, April, and May. The general procedure was for observers to walk pre-determined transects, usually inactive logging roads, scan cutovers with binoculars, and classify all deer observed. In June, however, most of the classification was done from vehicles. Most cutovers suitable for glassing in the study area were included in the inventory. Counts were done during a 1-week period in the middle of each month and only during the first and last 2 hours of daylight when deer were most visible.

During the summer months deer were classified as fawns, does, yearling bucks (spike antlers),and adult bucks (2+ years). Standard population statistics calculated were fawns:100 does, and % males of adults (including yearlings). Summer survival (%) of unmarked fawns was calculated as the observed fawn:adult doe ratio in August/fawn:adult doe ratio at birth x 100. The number of adult does was estimated by subtracting the number of yearling bucks observed from total does observed.

During spring, deer were classified as juveniles (10-11 month old fawns) or adults. The spring carryover (%) was calculated as fawns/(fawns+adults) x 100.

3.6. Deer Night Counts

Spotlight or night counts were conducted three times monthly from March until October. Representative portions of the study areas were searched using spotlights shone from a vehicle while travelling along predetermined road transects through cutovers. The driver counted on the left side of the road while the passenger counted on the right. Entire coverage of all transects was usually accomplished in one night. All replicates were usually done within a 1-week period, usually the last week of the month. The night counts are expressed as the number of deer per km of transect. As well as indicating the seasonal use of cutovers, the counts also provide an index to population density. I assumed, as did Jones and Mason (1983), that deer/km is linearly related to absolute density (deer/km^2). Details of the night count method and related statistical procedures are summarized by Harestad and Jones (1981).

3.7. Wolf Capture and Relocation

Wolves were captured in steel-jawed traps (No. 4 Newhouse double-spring trap and No. 3 Victor coil-spring trap). Trap sets consisted of either scent posts (scat, urine or both used as attractants), trail or blind sets, and bait (deer carcass) sets. A 1:1 mixture of ketamine/Rompun (100 mg/ml), administered via a jab stick or dart gun (Capchur Inc.), was used to immobilize captured wolves. Each wolf was sexed, aged, weighed, and standard body measurements taken. Wolves old enough to be neck collared were outfitted with a radio-transmitter (Telonics Inc.) that operated in the 150-151 mHz range, and then released. A more detailed description of the capture procedures can be found in Youds and Stordeur (1980).

Relocation procedures of tagged wolves from the ground were the same as those described for fawns. If the wolves could not be found, aerial searches from fixed-winged aircraft (Cessna 180 on floats) or helicopter (Jet Ranger) were used. The antenna was horizontally mounted on the wing strut of the plane or on the helicopter skids. After locating the signal, the pilot was instructed to circle inwards until the source of the signal could be pinpointed to a sidehill, timber patch, cut block or some other recognizable feature. The date, time of day, animal state (active or inactive radio signal), estimated accuracy, and habitat type were recorded.

Radio-tagged wolves were located on various schedules depending on the time of year, accessibility to the wolves, and the value of the information for assessing predation effects on deer recruitment. Generally, I attempted to relocate wolves daily from June until September, and as frequently as possible during the remainder of the year.

Radio-locations were plotted on 20-chain maps. Locations of radio-tagged pack wolves were combined to estimate wolf pack home ranges. If only one wolf was collared from a pack, its home range was assumed to represent the pack's home range, unless scat transects indicated otherwise. Using the computer home range program developed by Harestad (1981), 100%, 90%, and 50%

wolf pack home range sizes were calculated. The 100% home range included all locations and was considered synonymous with the pack's territory. The 90% home range included the closest 90% of the locations and identified an area of more concentrated use. The 50% home range included only the closest 50% of the known locations and identified the core area of use. Home sites (den and rendezvous sites) were located by repeated locations of radio-tagged wolves at a particular site, and by eliciting howling responses through human imitations of howls (Harrington and Mech 1979).

The term "buffer zone" is used to refer to areas of territory overlap (Mech 1977b). "Summer" wolf use is defined as April 1 through September 30, to coincide with home site occupancy by packs; "winter" as October 1 through March 31, when wolf packs travelled most extensively (Cf. Mech 1977a).

3.8. Scat Transects for Wolves and Black Bears

Inactive logging roads greater than 0.5 km in length were initially cleared of wolf and bear scats in May 1980. These roads, referred to as scat transects, were resurveyed monthly from April until October, and in January and March 1981. A pick-up truck or motorcycle was driven slowly along each transect to search for scats. Each transect was checked twice to ensure that few were missed. Every scat was identified and recorded to species (wolf or black bear), classified to age, and either collected or removed off the road. The criteria used in aging scats were: very fresh - recently deposited (usually less than 1 day old); fresh - moist (1 to several days old); medium - dried (1 day to several weeks old); leached - mostly hair remaining (probably > 1 month old); bleached - white and old (also probably > 1 month old); and old - amorphous or crumbly and flat (probably several months to one year old). Cougar scats could not be reliably separated from wolf scats. However, cougars did not appear to be common and aside from bear scats, I believe that most, if not all of the scats collected, were from wolves. Scat transects were stratified by 50%, 50-90%, and 90-100% home range boundaries of wolf packs. If scat densities (no. scats/km of transect/month) were highest in the 50% home range and lowest in the area encompassed by 90% and 100% boundaries, it was assumed that the radio-tagged wolf's movements were representative of the pack's territory.

3.9. Food Habits of Wolves and Black Bears

Scats were collected from scat transects as well as incidentally during the course of other work. Randomly collected scats were compared to transect scats to ensure that the age of the scat could be dated to the correct month. Generally the scat was only collected if it was very fresh. In 1981, the contents of bear scats were recorded in the field, and collected if the scat contained ungulate hair.

Wolf scats were autoclaved or oven dried at 100-110 C for 2-3 hours to kill *Echinococcus granulosa* ova (Bowan 1978; W. Samuels, pers. comm.). Several hair shafts were extracted from each scat and identified macroscopically from known hair samples if possible, otherwise microscopic techniques were used (Scott 1979; Kennedy and Carbyn 1981; Becker 1982). The regression

equation developed by Floyd *et al.* (1978) was used to relate wolf scat content to the relative numbers of adult deer and fawns consumed during June, July and August:

$$y = 0.38 - 0.2x$$

where y is the kilograms of prey per collectible scat and x is the average weight (kg) of a given prey type.

Collected bear scats were air dried and their content classified as either green vegetation, fruit (berries), insect, or ungulate. Only the number of food items, rather than the % occurrence of each food item in a scat was noted.

3.10. Statistical Analyses

The significance level for rejection of the null hypothesis was 5%. Statistical procedures follow Zar (1974). Spring carryover data were transformed with the arcsine transformation prior to regression analysis. In plotting the regression equation, predicted y values were transformed back to proportions resulting in a slightly curvilinear regression line (Zar 1974:186). Confidence intervals (CI) for fawn:doe ratios were calculated with the method outlined by Riney (1956). For spring carryover, CI were based on a normal approximation to the binomial. Finite correction factors were not applied to either fawn:doe ratios or spring carryover since population sizes were not known (Cochrane 1977). Prediction intervals (PI) are reported for linear regressions where the purpose was to predict future y's for x's one at a time (Tacha *et al.* 1982). For regressions of time series data, the first year of regression was standardized to 1. The standard error (SE) is given with means, unless stated otherwise.

4. RESULTS

4.1. Deer Reproduction

4.1.1. Fetal growth

Verme (1963) has shown that near the beginning of the last trimester of gestation, inadequate nutrition begins to retard fetal growth, thus increasing neonatal mortality. A growth curve for forehead-rump length of fetuses was established for deer at Northwest Bay by Thomas (1970). Figure 4 shows the forehead-rump length of fetuses measured in the Adam during the 2-week collection period in May and their fit to the growth curve for the last trimester of pregnancy. It is apparent, with the exception of two deer, one of which was a yearling, that the chronology of fetal growth in the Adam was very similar to Northwest Bay. None of the fetuses were obviously defective.

Since fetal growth appeared normal, birth dates of captured fawns were estimated from their body weight according to Figure 1 of Mueller and Sadlier (1980). The mean date of birth, 10±1 June, was similar to the mean date of 11-14 June reported for Northwest Bay by Thomas (1970).

4.1.2. Birth rate

The fetal rate of autopsied adult does in the Adam was 167 fetuses:100 does, similar to that reported from Northwest Bay and the Nimpkish Valley (Table 2). The one yearling female examined had one fetus, whereas 12 out of 13 yearlings at Northwest Bay and 3 out of 5 in the Nimpkish bore fetuses. Thus fetal rates of Adam-Eve does were considered typical for Vancouver Island.

Table 2. Fetal rates (no.of fetuses/100 does) for three different areas on Vancouver Island

Area	Adult	Yearling	Fawn
Adam River[a]	167 (15)[b]	100 (1)	0 (4)
Nimpkish Valley[c]	163 (27)	60 (5)	0 (10)
Northwest Bay[d]	167 (48)	92 (13)	60 (8)

[a] this study, M.U. 10-12, 13 (1980-81)
[b] sample size shown in parentheses
[c] Jones (pers. files), M.U. 11 (1972-73)
[d] Thomas (1983), M.U. 5-7 (1963-64)

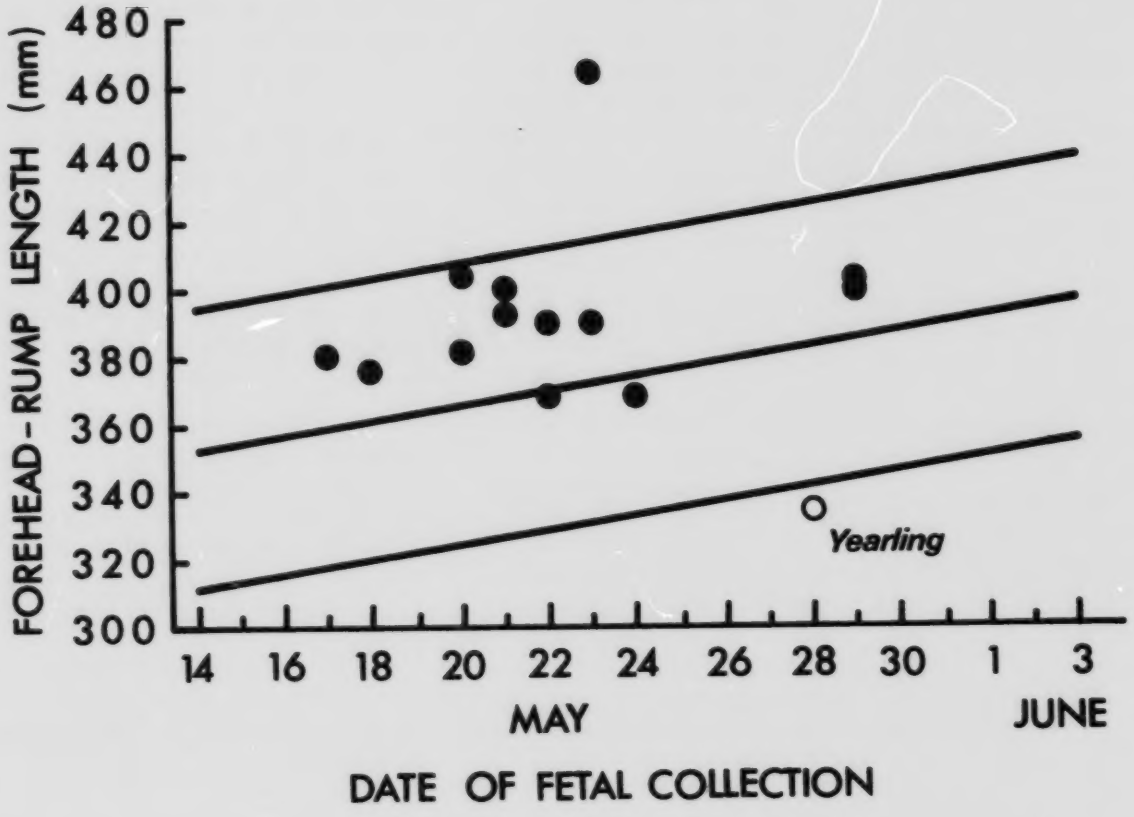

Figure 4. Relationship between forehead-rump length of 23 fetuses and date of collection in the Adam River. The average length was used for twin fetuses. The expected growth curve for the last trimester of pregnancy and 95% PI, as calculated from Fig. 22 of Thomas (1970), is also shown. The curve is described by the equation $y=-32.4 + 2.27x \pm 19.82$, where y is the forehead-rump length and x is the mean gestation age. Gestation age was converted to calendar date using the mean date of conception as November 25 (Thomas 1970).

To determine the birth rate (no. fawns born per 100 does), the age class structure of the doe population as well as age-specific reproductive rates must be known. This age class structure was estimated from the antlerless harvest, assuming that hunters did not select different age-classes of does and that all animals were equally vulnerable. Yearlings, however, are known to be more vulnerable to hunting and therefore this vulnerability must be corrected (Maguire and Severinghaus 1954; Taber and Dasmann 1954). To evaluate yearling vulnerability, the proportion of yearling does in summer classification counts was compared to the proportion in the kill. yearling females could not be distinguished accurately from adults by all observers during July and August, the number of females older than 2 years of age in the summer counts was calculated by subtracting the number of spike males observed (Appendix C). This assumed all spikes were yearling males and the sex ratio in yearlings prior to the hunting season was even. Examination of hunter--harvested deer in 1980 and 1981 indicated that 95% (n=62) of 1.5 males had spike antlers whereas only 10% (n=30) of 2.5-year-old males had spikes. Fawn sex ratios to 11 months of age appeared to be equal (Table 3), and summer classifications by B. Mason from 1976 to 1981 indicated an even yearling sex ratio prevailed 5 out of the 6 years. Thus both assumptions were considered valid. The proportion of yearling does was estimated at 21% in 1980 and 19% in 1981, or about 20% during the study period. Yearlings, however, comprised 37% of the doe harvest. Since yearlings appeared to be only slightly more vulnerable during the first weekend (38% of 34 does) compared to the second weekend (30% of 30 does) (x^2= 0.48, df=1, .25<p<.50), the yearling vulnerability factor was estimated at 1.8 (37/20). As adult fetal rates were similar to Northwest Bay, age-specific viable fetuses:100 does reported by Thomas (1983) were used to determine the birth rate. These are the recorded reproductive rates adjusted for a 3.3% fetal mortality rate. The adjusted female age structure based on a yearling vulnerability factor of 1.8 and age-specific reproductive rates is shown in Figure 5. This age structure is not stable and suggests increasing fawn and possible yearling mortality during the study period. The birth rate was estimated at 141 fawns:100 does, similar to the 138 fawns:100 adult does estimated at Northwest Bay by Thomas (1983). The slightly higher rate in the Adam is due to the correction for yearling vulnerability, which Thomas did not consider.

Table 3. Sex ratios for deer fawns in the study area, 1980-81

Age (months)	Male	Female	% Males	Chi-Square	Sig. Level
0[a]	12	13	48.0	0.04	0.75<p<0.90
.03-.25[b]	11	17	39.3	1.29	0.25<p<0.50
6[c]	20	21	48.8	0.02	0.75<p<0.90
11[d]	5	4	55.6	0.11	0.50<p<0.75

[a] fetal sex ratio
[b] sex ratio of captured fawns
[c] sex ratio of fawns in hunter harvest
[d] sex ratio of fawns in spring deer collection

Figure 5. Age-class structure of female deer in the Adam-Eve. The open bars are the observed proportion of each age-class in the hunter harvest. The shaded bars represent the corrected proportion, based on a yearling vulnerability of 1.8. The numbers above each bar are the estimated age-specific viable fetuses:100 does from Thomas (1983). Total sample size = 71 (1980-81 combined).

4.2. Fawn Mortality

4.2.1. Extent and timing of mortality

Fawn:doe ratios showed a linear increase from June to August as fawns became less secretive and more visible (Fig. 6). Fawn:doe ratios in July and August, but not June were significantly different between years (June: X^2=1.61, df=1, .10<p<.25; July: X^2=8.31, df=1, .001<p<.005; August: X^2=10.10, df=1, .001<p<.005). Assuming 141 fawns:100 adult does at birth and no doe mortality, fawn mortality by the end of August was 61% in 1980 and 79% in 1981.

Twenty-eight fawns were radio-tagged during the study, 15 in 1980 and 13 in 1981. Two of the fawns were noticeably sick when captured (1 in 1980, 1 in 1981). Since these were the only fawns captured in July (healthy fawns by this date were too difficult to capture), they were not included in the mortality statistics. In five instances, radio-collars fell off prematurely while four others apparently malfunctioned. Fawn mortality from June to August was estimated at 55% in 1980 and 71% in 1981.

Despite the limitations of both the age ratio and telemetry methods, the two independent mortality estimates appeared similar within years. This suggests marking techniques did not directly or indirectly affect mortality by predisposing radio-tagged fawns to predators (White *et al.* 1972). The slightly higher mortality rates, based on the age ratio method, is contrary to what would be expected if substantial doe mortality also occurred during the summer (Connolly 1981). This discrepancy was likely due to some fawns hiding during the August surveys. Hines (1961) showed that the proportion of observed black-tailed deer fawns in an Oregon herd increases linearly from June to September. Jones and Mason (1983) also suggested that wolf activity may cause does to keep their fawns hidden more often. The apparent increase in fawn mortality in 1981, although probably real, is partially confounded by the distribution of radio-tagged fawns and disproportionate classification of deer in low wolf activity areas in 1980 and near wolf home sites in 1981 (see 4.6). Because of this, I suspect mortality was underestimated in 1980 and overestimated in 1981. Due to difficulties in trying to correct mortality estimates for these biases, and small sample sizes for both years, the mean of the two radio-telemetry mortality estimates, 63%, was considered the best estimate of fawn mortality by the end of August.

The chronology of fawn survival during the first 6 months, based on the radio-collared sample, is shown in Figure 7. Sample sizes were inadequate to calculate monthly survival rates after this date. Survival rates were constant during June and July (monthly p_s = 64%) but increased to 92% in August, 100% in September and October, and then declined to 78% in November. The cumulative survival rate from June to December was approximately 30%.

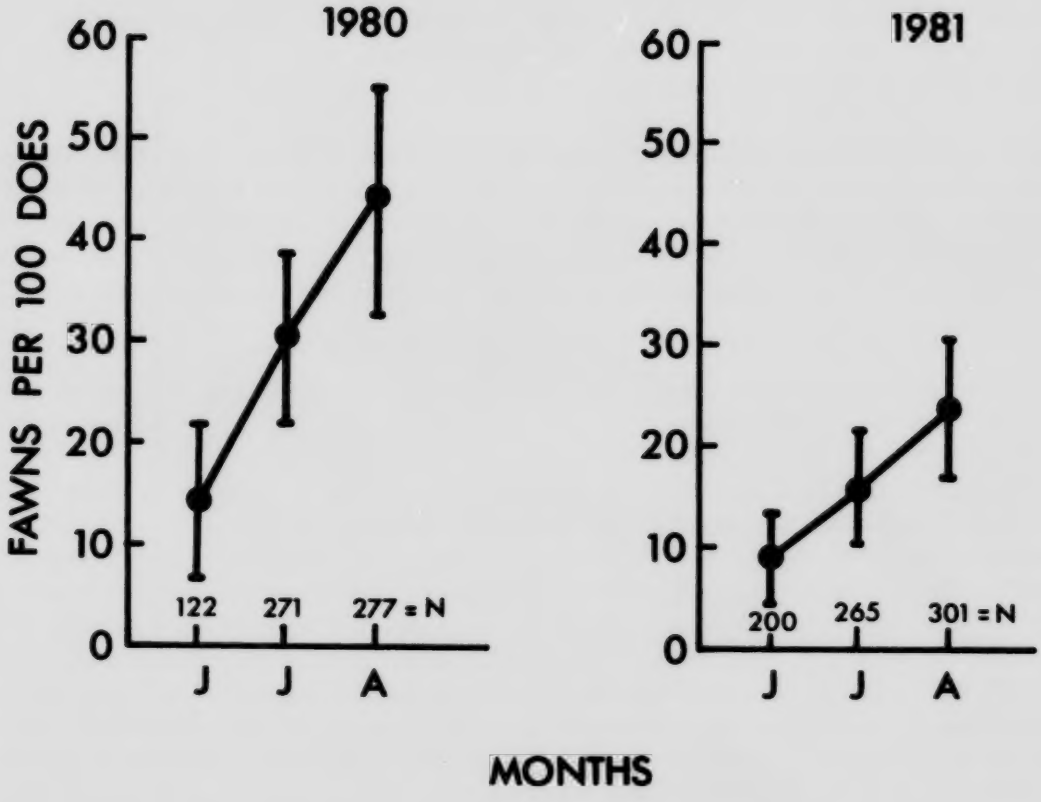

Figure 6. Observed fawns:100 does in June, July, and August. Both adult and yearling does are included. Vertical bars represent 95% CI.

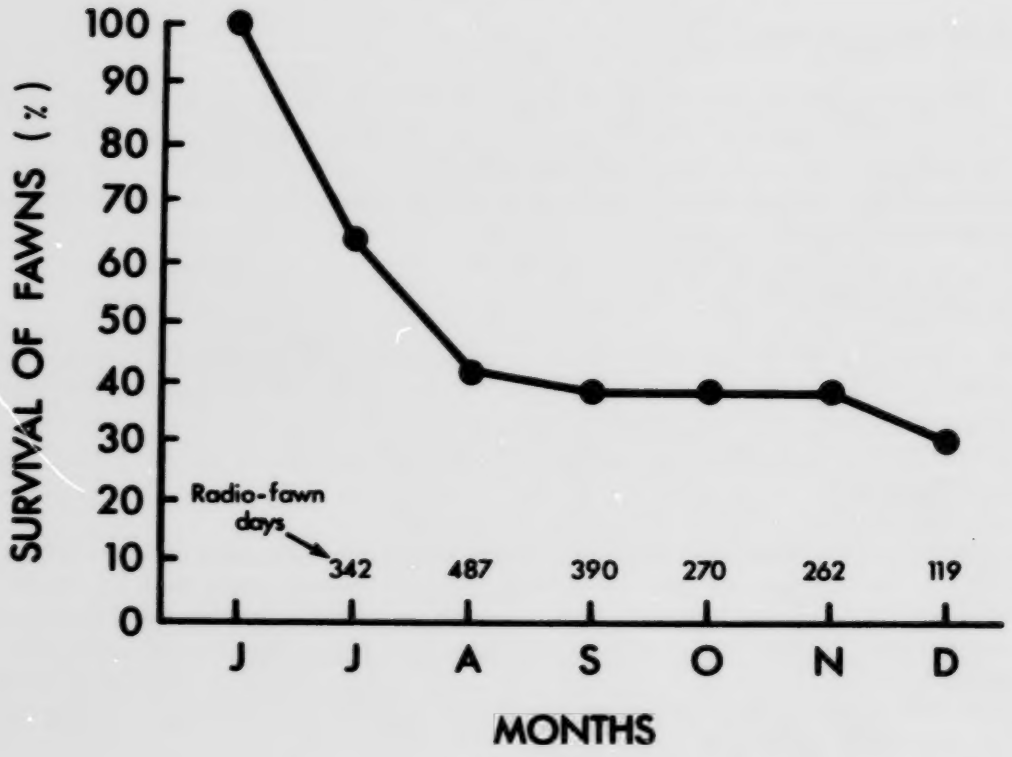

Figure 7. Cumulative percent survival of radio-tagged fawns from June to December (1980-81).

Using the relationship shown in Figure 6, summer fawn:doe ratios in the Adam for 1975, 1976, and 1977 were standardized to August fawn:doe ratios by increasing July fawn:doe ratios by 1.5 (Fig. 8). The significant decline in August fawn:doe ratios ($F=10.43$, df=1 and 5, $.01<p<.025$) since 1975 supports the observed decline in spring carryover since 1976 (Fig. 9) ($F=5.90$, df=1 and 5, $.05<p<.10$). It also supports the results of the telemetry sample that summer was the most important period influencing recruitment.

4.2.2. Causes of mortality

The fate of the radio-tagged fawns are shown in Table 4. Of 14 fawns that died, eight were attributed to wolf predation, two to accidents, one to bear predation, one to disease, one to malnutrition, and one to hunting. In addition, two fawns collared in July were sick at capture and subsequently died - one to disease and the other to malnutrition. Each of these mortality factors are examined below.

4.2.2.1. Malnutrition

Two radio-tagged fawns apparently died of malnutrition. FN 6330(2)-81 had diarrhea when captured on 11 July 1981 and died 2 days later. Kramer *et al.* (1971) reported diarrhea and death occurring in captive mule deer fawns. Bacteria recovery from this fawn was insignificant and the cause of death was attributed to malnutrition. FN 6555-80 died on 22 April 1981, also from malnutrition.

No debilitated fawns were observed during classification counts. The mean capture weight of fawns was 3.3 ± 0.47 kg and was not significantly different between years ($t=-0.47$, df=25, $p<.50$). Mueller and Sadlier (1980) reported a mean birth weight of 2.7 ± 0.04 kg for healthy fawns born to well fed does. Considering some fawns may have been several days old when captured, weights of Adam-Eve fawns appeared comparable. The mean capture weight of fawns that survived the summer (3.4 ± 0.32 kg) was also similar to the mean capture weight of those that died during this season (3.2 ± 0.22 kg) ($t=0.57$, df=20, $p>.50$).

To determine the potential importance of malnutrition as a mortality factor, the physical conditions of does, as well as fawns, was assessed. Tissue samples from collected does showed no obvious deficiencies. The KFI of female deer from the Adam-Eve was not significantly different from the Nimpkish Valley in 1973-74 ($t=-0.22$, df=23, $p>.50$). Rochelle (1980) included fawns with adults in his sample so it was not possible to test for differences in fawns only. Since no baseline data on CONINDEX value of deer were available from Vancouver Island, the CONINDEX of deer from the Adam-Eve fawns was tested against mule deer from Steens Mountain, Oregon (*O. h. hemionus*) (Fig. 10). CONINDEX values of Adam-Eve fawns were significantly higher than those from Steens Mountain ($t=2.04$, df=56, $.02<p<.05$), although no significant differences existed between does ($t=0.07$, df=204, $p>.50$). CONINDEX values of five Adam-Eve males were also similar to Adam-Eve females ($t=0.18$, df=17, $p>.50$). Trainer *et al.* (1979) proposed the following classes for rating fawn condition based on the CONINDEX: good condition = > 50; fair - 49-20; and poor - < 20. Assuming this is applicable for coastal black-tailed deer, spring fawns were in fair condition. Field-dressed weights of female deer shot by hunters in the Adam-Eve are shown in Figure 11. Age- and sex-specific mean weights attained were comparable to mean weights on northern Vancouver Island from 1957-64, when hunter harvests and presumably populations were increasing (Hatter 1980). A similar analysis for males also showed no discernible differences.

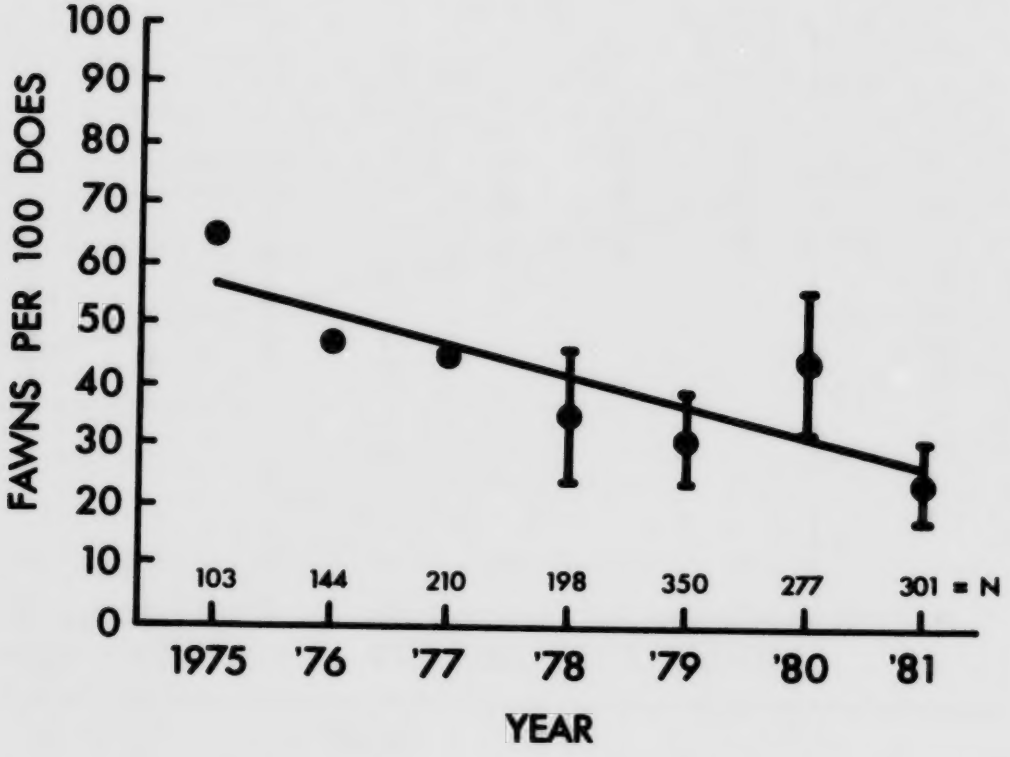

Figure 8. Trend in fawn:100 doe ratios in the Adam-Eve from 1975-81. The regression line is described by the equation $y=61.3 - 4.98x \pm 8.24$. Vertical bars represent 95% CI for August fawn:doe ratios. July fawn:doe ratios (1975-77) were standardized to August fawn:doe ratios by multiplying by 1.5. Since these are projected estimates, 95% CI were not applied.

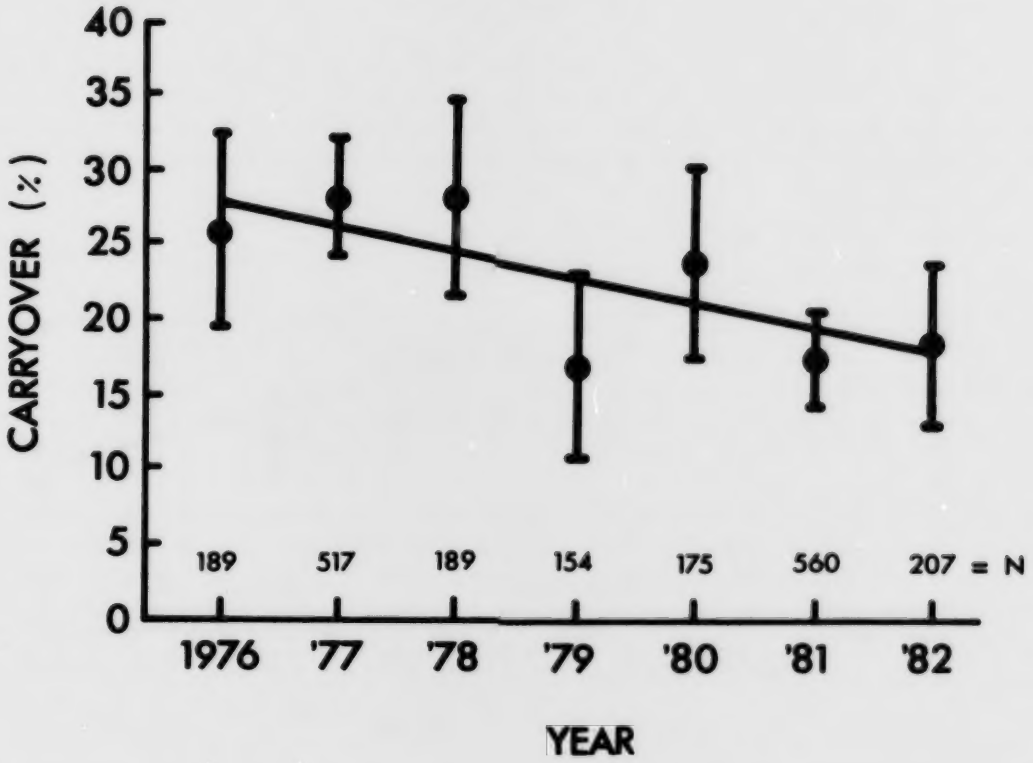

Figure 9. Trend in spring carryover in the Adam-Eve from 1976-82. The regression line is described by the equation arcsine square-root $y = 33.0 - 1.17x \pm 2.55$. Vertical bars represent 95% CI.

Table 4. Results from 26 radio-collared fawns in the Adam River watershed (1980-81)

	No. of Fawns	
	Summer[a]	Fall-Winter-Spring[b]
Predator-Excluded Mortality		
Accident	2	
Disease	1	
Hunting		1
Malnutrition		1
Subtotal	3	2
Predator-Involved Mortality		
Wolf- positively identified	7	
probable	1	
Black Bear- positively identified	1	
	9	
Survivors	9	2
Transmitter Failure	3	1
Collar Slip/Breakage	2	4
Subtotal	14	7
Total	26	9

[a] June - August
[b] September - May

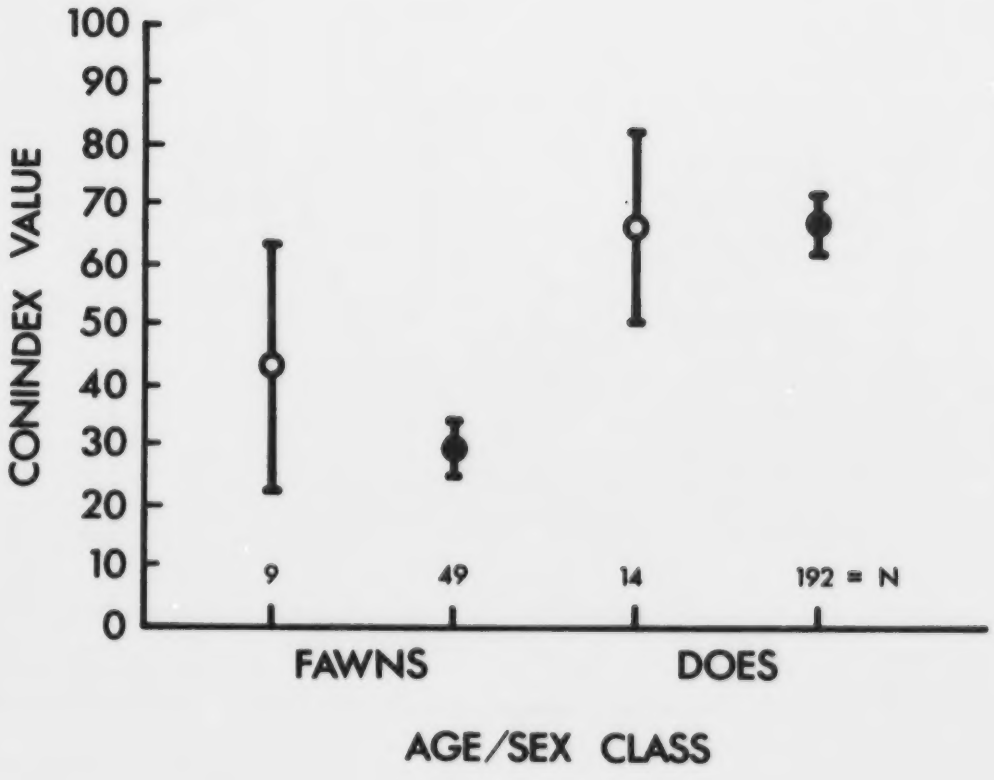

Figure 10. Condition index (CONINDEX) values for fawns and does in the Adam River (○)(1980-81) and mule deer from Steens Mountain, Oregon (●) (Trainer *et al.* 1979) during late spring. Vertical bars represent 95% CI.

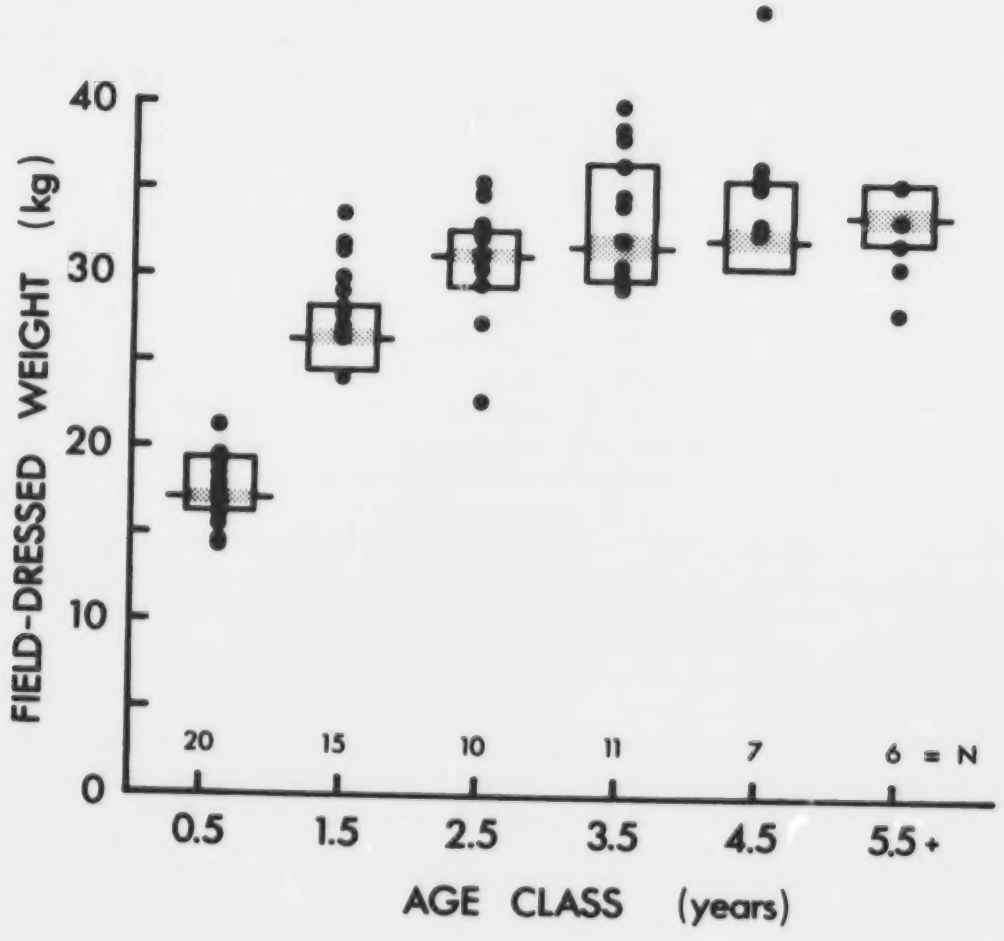

Figure 11. Field-dressed weights (●) by age of female deer from the Adam-Eve (1980-81). The mean ± SE (shaded rectangle) and range (open rectangle) in weights for female deer from northern Vancouver Island (1957-64) are also shown.

At Northwest Bay, the most important factor affecting the abundance of fawns in August was the severity of the preceding winter (Smith, no date). From 1954-68, a highly significant correlation ($r=-.78$, $df=11$, $.001<p<.002$) existed between August fawn:doe ratios and cumulative snowfall the preceding winter. Unfortunately, neither weather nor herd composition records were extensive enough to test for a similar weather effect on recruitment in the Adam-Eve prior to the increase in the wolf population. No correlation, however, was found between August fawn:doe ratios and cumulative snowfall from 1976 to 1981 ($r=.33$, $df=5$, $.20<p<.50$). Cumulative snowfall at Port Hardy based on the last 20 years indicates that weather severity on northern Vancouver Island has been below average since 1976 (Fig. 12).

4.2.2.2. Disease and parasites

Enteropathogenic bacteria were isolated from 17 of 22 radio-tagged fawns. The most prevalent bacterium isolated was *Escherichia coli*, 13 swabs having heavy levels, two moderate, and two light. The significance of the heavy *E. coli* loads could not be ascertained since certain strains constitute normal flora for deer (M. Hewitt, pers. comm.). One fawn had scant *Pseudomonas* spp. but was not considered significant (R. Lewis, pers. comm.). Tests for *Salmonella/Arizona* spp. were negative in every case. No other bacteria were isolated from fawns.

Observations of fawns at the collaring site gave no indications of disease-related problems, except for two possible exceptions. FN 6328(2)-80 and FN 6327-81 both had blood around the rectum when captured. FN 6328(2)-80 was collared on 7 July 1980 and died 12 days later. However, FN 6327-81, which was collared on 20 June 1981 was monitored for 71 days before transmitter failure. It was visually observed three times and appeared healthy each time.

Two fawns likely died from disease-related deaths. A deer adenovirus was isolated from FN 6328(2)-80, but nothing was found in the literature to suggest its significance in black-tailed deer (M. Hewitt, pers. comm.). In other species, adenoviruses can be related to viremia and death, so it is possible that it may have been important in this case. The second fawn, FN 6326-80, was collared on 19 June 1980 and died 14 days later. The diagnosed cause of death was coliform enteritis, indicating that it likely died from a pathogenic *E. coli* strain. The fecal swab from this fawn had heavy *E. coli*. A third fawn, FN 6328-81, which died while trapped under a tree stump, also had acute coliform enteritis. In this case, it was likely that the fawn was not receiving adequate nutrition and thus its gastrointestinal resistance to infection may have been lowered. It is known that *E. coli* can cause death in domestic animals if they are subjected to either stress or unfavourable nutritional factors (Sojka 1965, cited by Ballard and Taylor 1978).

It seems unlikely that pneumonia, caused by inclement weather during fawning, was involved in deaths caused by bacteria or viruses. Although total rainfall in June 1981 (161.0 mm) was much higher than the normal (114.8), no respiratory-related deaths were recorded. Smith (no date) analyzed various summer weather parameters and was unable to find a significant relationship with August fawn:doe ratios at Northwest Bay.

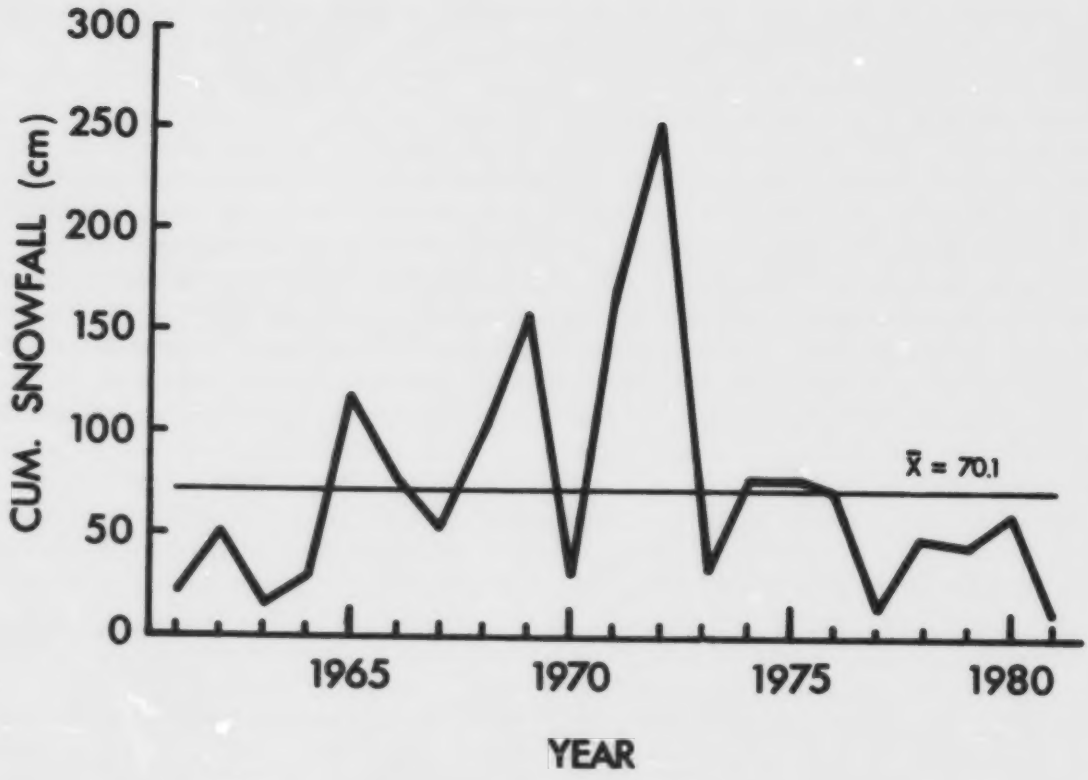

Figure 12. Cumulative snowfall at Port Hardy airport, 1960-61 to 1980-81 (61 refers to 1960-61 winter etc.).

No obvious evidence of external parasites was found on radio-tagged fawns or autopsied deer. Internal parasitic infestations, with the exception of *Cysticercus tenuicollis* and *Echinococcus granulosus*, were also low. *C. tenuicollis* was a common parasite in the deer examined. Cowan (1946) reported high levels of this parasite on Vancouver Island and the adjacent mainland (82.5%, n=40). In the study area, about 16% of the deer were infected with *E. granulosus* (Table 5). These infection rates are much higher than those reported by Cowan (1946) who only found one instance of the parasite in 65 deer examined but are comparable to some deer herds in California (Brunetti and Rosen 1970). No fawns, however, were known to be infected and only one was suspected. Since multiple infections were rare, with none observed in fawns, it seems doubtful that this parasite could have affected deer vigor or recruitment.

4.2.2.3. Accidents

Of two radio-tagged fawns that died from accidental deaths, one was run over by a vehicle on a logging road on 20 June 1980, 9 h after tagging, while the other apparently crawled into a hole under a tree stump in a cutover and became trapped. The radio signal from the second fawn was on mortality mode at 2200 h on 20 June 1981. The fawn was retrieved out of the hole and placed under a hemlock sapling. Although still alive, it was unable to stand. By 0730 h on 21 June, the fawn was dead, apparently due to exposure and/or starvation. Autopsies of both fawns were inconclusive as to whether they had been predisposed to these accidents as a result of poor physical condition. Both, however, seemed healthy when captured and appeared to have re-established bonds with their dams, prior to their deaths.

Table 5. Incidence of hydatid infection in deer from 1980-81[a]

Age Class	No. Sampled	No. Infected	No. Suspected Infected	% Infected[b]	% Suspected Infected[c]
0.5	25	0	1	0	4
1.5	49	7	5	16	24
2.5	15	4	2	31	40
3.5	10	1	1	11	20
4.5	5	1	0	20	20
5.5+	12	4	1	36	42
Total					
0.5-5.5+	116	17	10	16	23
1.5-5.5+	91	17	9	21	29

[a] includes deer from spring field autopsies and from hunter check station.
[b] % infected = no. infected/(no. sampled - no. suspected infected) x 100.
[c] % suspected infected = (no. infected + no. suspected infected)/no. sampled X 100.

4.2.2.4. Hunting

One radio-tagged fawn was shot by a hunter during November 1980, and another fawn radio-tagged in 1980, which subsequently had lost its collar, was shot as a yearling in 1981. It was not possible to measure the impact of hunting on fawn mortality from the radio-tagged sample since few collared fawns were present during the hunting season. Also it is not know what bias the collar may have created in hunter selectivity for fawns. Several hunters reported seeing radio-tagged fawns but did not shoot them, whereas the hunter who killed the fawn in 1980 was unaware of the collar before shooting.

Hunters appear to have selected fawns since 1976 (Fig. 13). A quadratic equation indicated selectivity for fawns increased from 1975 to 1979 and then declined during 1980 and 1981 ($F=12.23$, $df=2$ and 4, $.01<p<.025$). The magnitude of selection, however, may have been overestimated if August fawn:doe ratios underestimated the true proportion of fawns to does. Hunter selectivity was not significantly correlated with carryover the following spring ($r=-.63$, $df=5$, $.10<p<.20$). Also carryover in the Adam-Eve and an adjacent watershed (White River, M.U. 10-8) from 1976-82 were correlated ($r=.75$, $df=5$, $p=.05$), despite no antlerless season in the latter (B.C. Fish and Wildlife Branch, unpubl.). This suggests that fawn hunting mortality was not sufficient to reduce recruitment substantially.

4.2.2.5. Predation

Eight radio-tagged fawn mortalities were attributed to wolf predation (three females, five males), one to bear predation (female), and none to cougars. All of the predator-involved mortalities occurred prior to the end of August. The remains of radio-tagged fawns killed by wolves varied from partially eaten, buried fawns to evidence of a few fresh blood spots on the radio-collar. Of seven fawns positively identified as wolf kills, the remains of three fawns were cached (two in cutovers, one in mature forest). In each case, the anterior portion of the fawn was left intact, the body having been severed just behind the rib cage. Two of these fawns had been bitten in the head, as indicated by extensive hemorrhaging associated with puncture wounds to the skull. Garner *et al.* (1976) reported coyotes (*Canis latrans*) burying white-tailed deer (*O. virginianus*) fawn carcasses in a similar manner. In two other cases, only the collar and pieces of the cranium, mandible, and small patches of the hide remained. In the sixth case, the hide had been scattered over a 100 m^2 area. The ear tags and part of the ear, one hoof tip, and the tail were found. In the final case, only two patches of fawn hair remained. In the single bear-related mortality, aside from the radio collar, only the ear-tags and part of the cranium were found.

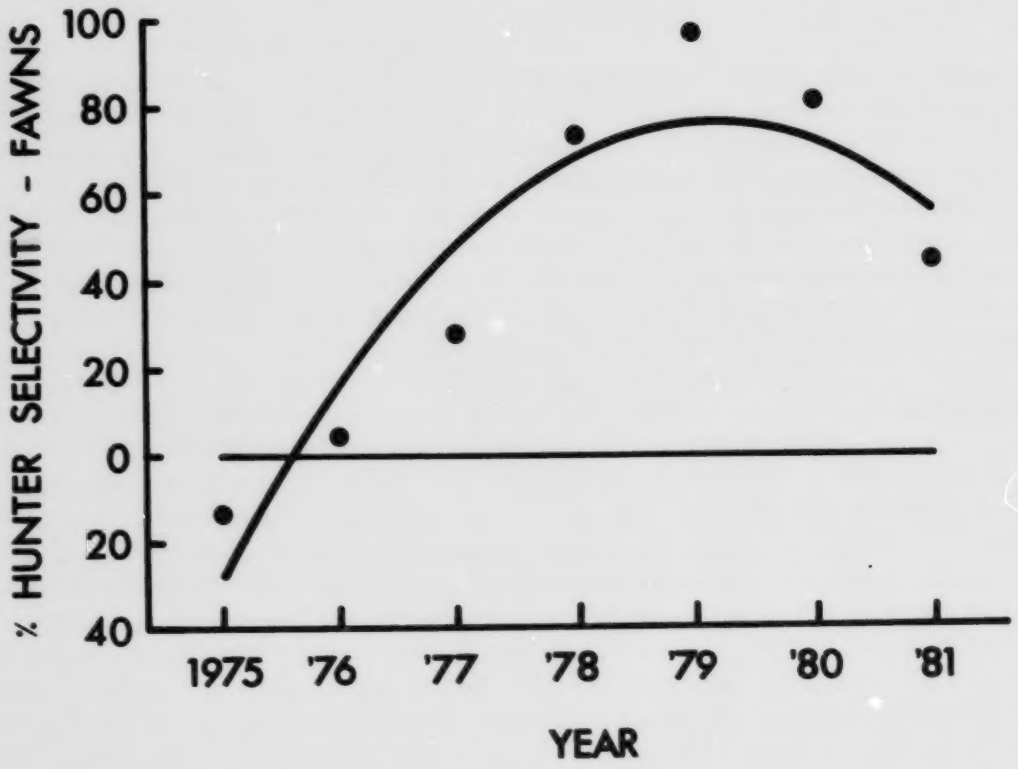

Figure 13. Hunter selectivity for fawns from 1975-81.

The possibility that these fawns had been scavenged rather than killed seems slight. Usually fawns were retrieved within 24 hours of dying, most within 12 hours or less. One exception was a fawn that died on 20 July 1980. Due to excessive bounce in the area and inexperience with radio-telemetry equipment, I was unable to locate the fawn until 22 July. During this interval the fawn had not been disturbed by any predator, despite being close to a travel route used by the Upper Adam wolf pack. In July 1981, I placed a highway fawn kill within 300 m of an active rendezvous site of the Upper Adam wolf pack, being careful not to contaminate the carcass with human scent. Two days elapsed before wolves removed the fawn and transported it back to the rendezvous site. Thus it seems likely that I was able to locate and retrieve dead fawns prior to wolves or bears finding them. Other investigators have also reported the incidence of scavenging of radio-tagged fawns by mammalian predators to be low (Cook *et al.* 1971; Trainer *et al.* 1981).

Food habits of wolves and black bears were evaluated from scat analysis. Unfortunately, hair shaft diameters and medulla patterns of deer fawns and elk calves showed sufficient overlap to make separation of deer fawns from elk calves difficult and I was unable to consistently separate the two species from available keys. However, elk were relatively uncommon in the study area. I observed few calves within the Upper Adam wolf pack territory and none within the Lower Adam pack territory. It is therefore probable that most of the juvenile cervid remains were deer fawns and not elk calves. Scott and Shackleton (1980) indicated that elk calves were the predominant component of the wolves summer diet in the study area in 1978. However, their analysis is inconsistent with elk distribution data collected between 1975 and 1979 (Hebert *et al.* 1982). In the following analysis, juvenile cervids are referred to as fawns, although a small proportion may have been elk calves.

Wolves fed primarily on deer from May to September with beaver and elk being minor prey items (Fig. 14). The presence of some fawns in the diet during May may be from early born fawns or fetuses. The proportion of fawns recorded in the diet in September is a minimum since many of the fawns had started to develop the winter adult deer pelage. Thus the importance of fawns in the diet could only be traced during the June - August period. The proportion of fawns to adult deer was similar for both 1980 and 1981 (June: $x^2=0.01$, df=1, $.90<p<.95$; July: $x^2=0.21$, df=1, $.50<p<.75$; August: $x^2=0.02$, df=1, $.75<p<.90$). Combining both years, the proportions were significantly different between months ($x^2=45.71$, df=2, $p<.001$). Subdividing the analysis indicated that fawn proportions during June and July were not different ($x^2=0.07$, df=1, $.75<p<.90$), and pooling these months indicated that the August proportion was significantly less ($x^2=42.00$, df=1, $p<.001$).

The chronology of fawn mortality was closely related to the frequency of occurrence of fawn remains in wolf scats (Fig. 15). Assuming adult deer weighed 42.2 kg (Rochelle 1980:249) and fawns weighed 2.8, 7.0 and 13.0 kg in June, July, and August, respectively (Mueller and Sadlier 1980), the ratio of fawns to adults in the wolves diet, based on relative weights, were 9:1 in June, 5:1 in July, and 1:1 in August. This indicates fawns, rather than adult deer, represented the major prey item taken during summer. Scott and Shackleton (1980) reported deer were also the primary food item in the wolves winter diet.

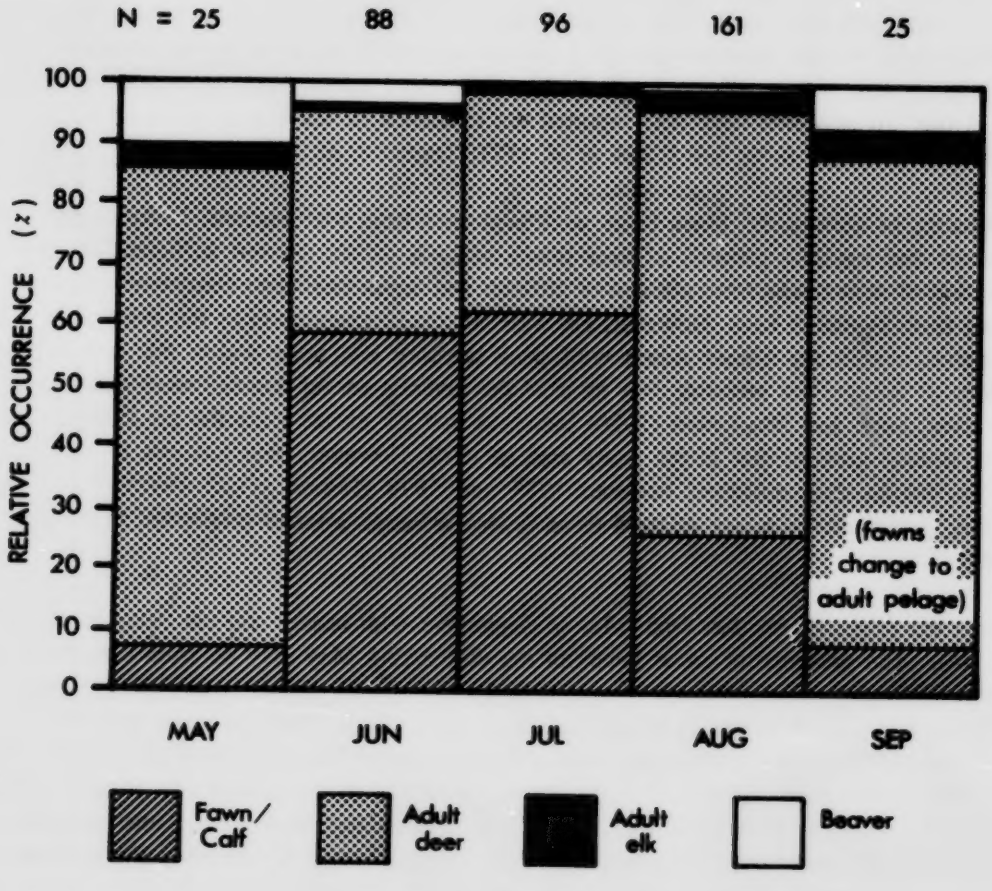

Figure 14. Relative frequency of occurrence of food items in wolf scats, May- September (1980-81). Fawn remains can only be reliably distinguished during the June-August period. N = no. of scats.

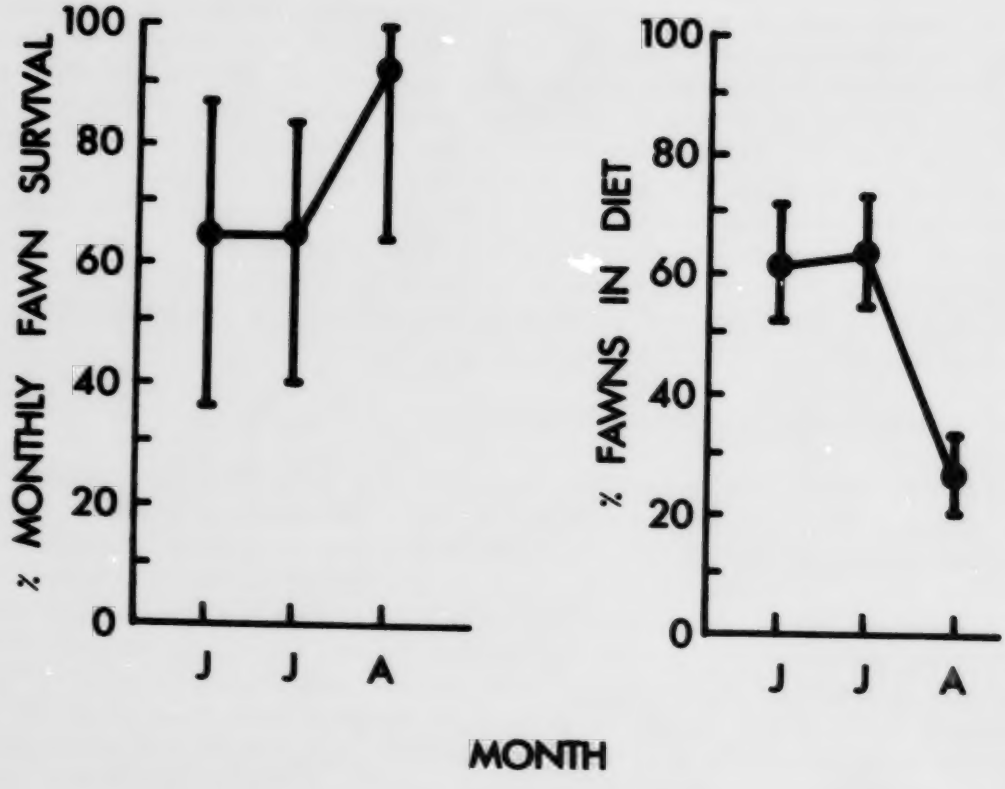

Figure 15. Relationship between monthly fawn survival and the frequency of occurrence of fawns in wolf scats. Vertical bars show 95% CI.

Black bears appeared to feed primarily on green vegetation during May and June, shifting to fruits (especially berries of *Vaccinium* spp. and *Rubus spectabilis*) and insects (Formicidae) in July and August (Cf. McIlroy 1970; Lloyd 1979) (Fig. 16). The small sample size in September precludes interpretation of the diet for that month. Fawns were a minor component in the summer diet with 7% of the food items in June containing fawn remains, 3% in July and none in August. Overall, only 7% of 406 summer bear scats contained fawn remains. Longhurst *et al.* (1952) reported that 12% of the bear scats in California contained fawn remains and Schwartz and Mitchell (1945) found 8% in scats from Washington. The bear food habits analysis, however, may be biased. Only scats on logging roads were analyzed. Thus only the cutover habitat types were sampled. However, this bias should have overestimated the relative importance of fawns in the bears diet since fawns appeared to occupy cutovers most frequently during summer (see 4.3). Although the peak in bear scat densities occurred in June, it was probably related to green-up of cutovers, rather than fawning (Fig. 17). Wilton (1983) also noted that prey "skinning" or everting of the hide could result in a lack of hair in scats from bears feeding on neonatal ungulates. No evidence for this, however, was found. One radio-tagged fawn killed by a bear appeared to be almost completely consumed. Scats containing fawn remains often had an abundance of hair. Hoofs were also occasionally present in the scats suggesting near complete utilization of fawns by bears. The low use of fawns by bears may have been related to the lack of specific fawning habitats, which could concentrate fawns after birth.

4.3. Fawn Home Ranges and Seasonal Movements

Harestad (1979) defined three seasonal home ranges for adult black- tailed deer, corresponding to spring (March to June), summer (June to November), and winter (November to March). For fawns, I calculated natal (June - August) home ranges. The average natal home range for nine fawns with 10 or more radio-locations was 23 ± 7 ha. These home ranges are smaller than reported in other studies (mule deer: 257 ha [Steigers and Flinders 1980], 73 ha [Geduldig 1981]; white-tailed deer: 53 ha [Garner and Morrison 1977]). The smaller size of the natal home ranges for black-tailed deer versus mule or white-tailed deer is consistent with body size relationships as discussed by Harestad and Bunnell (1979). It may also be due to the small number of radio- locations per fawn (Appendix F). Movements tended to be greater in August as fawns became more active (Fig. 18), although none of the fawns ever left the study area. Eighty-six percent of 237 telemetry locations in 1981 were in cutovers. Only one fawn showed evidence of long range movements during the June-August period, two of the radio-locations being located well outside its apparent home range (Fig. 19). Two fawns killed by wolves, however, were also located well outside their known home range (Fig. 20). I suspect in each case the fawns were transported to these sites by the wolf.

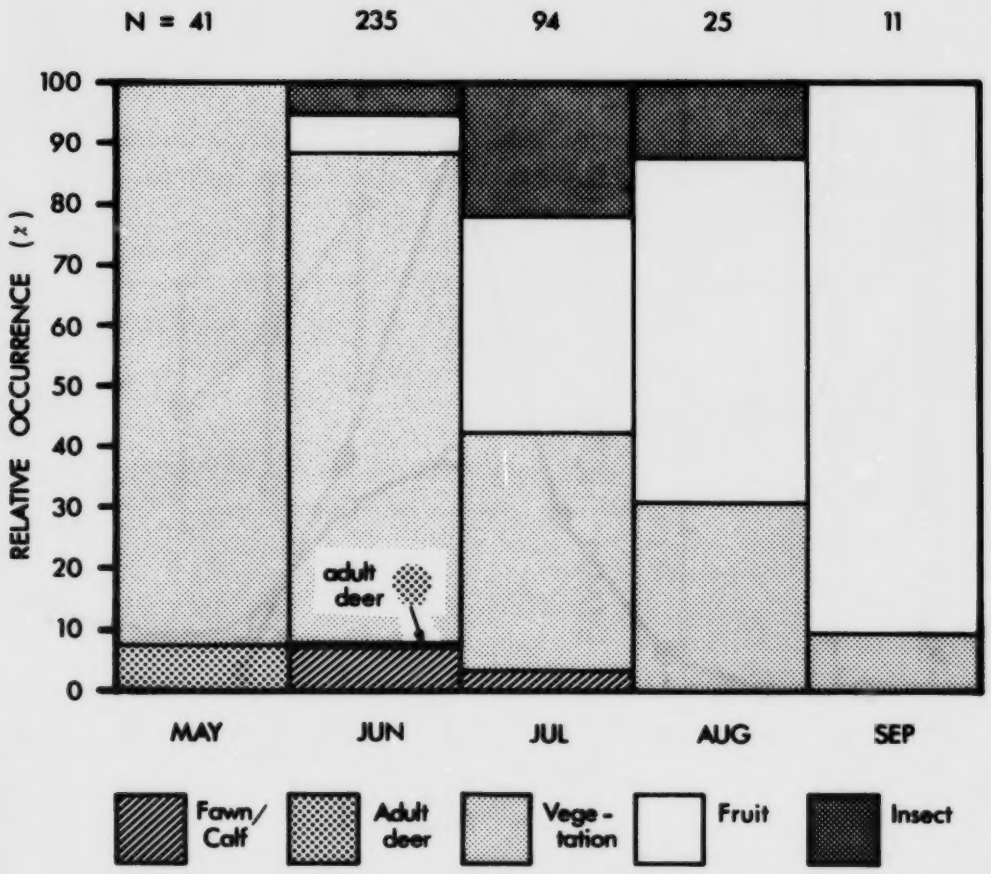

Figure 16. Relative frequency of occurrence of food items in black bear scats, May-September, 1980-81. N = no. of scats.

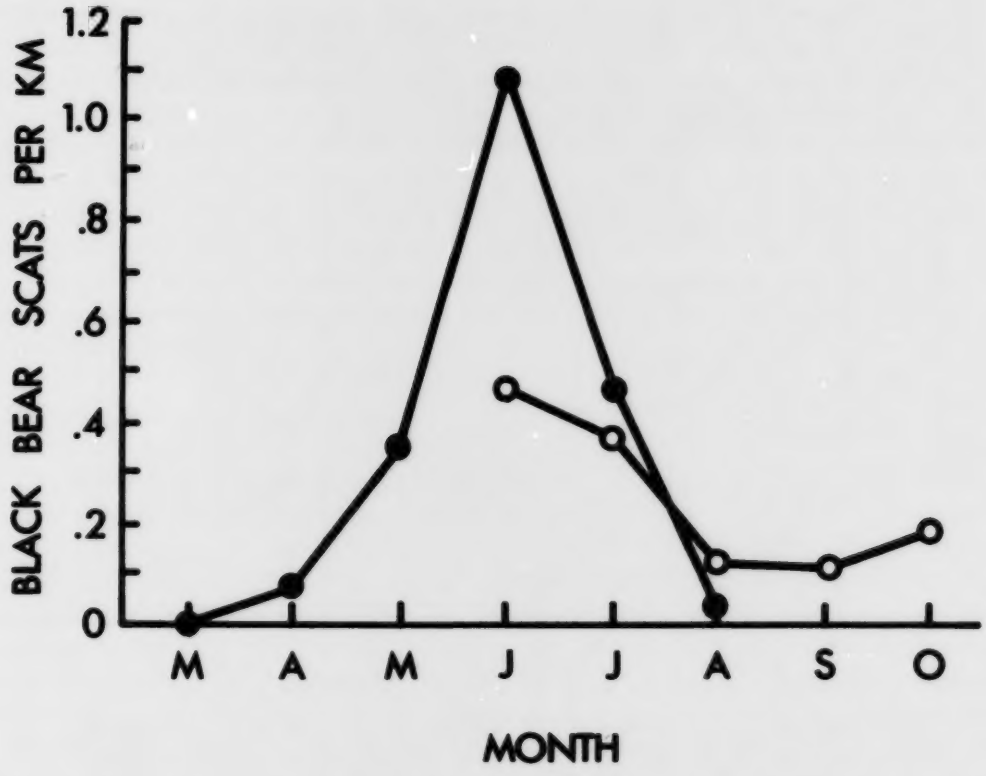

Figure 17. Relative use of cutovers by black bears from June-October 1980 (O) and March-August 1981 (●), based on scat transects. Total no. of km/month = 98.5.

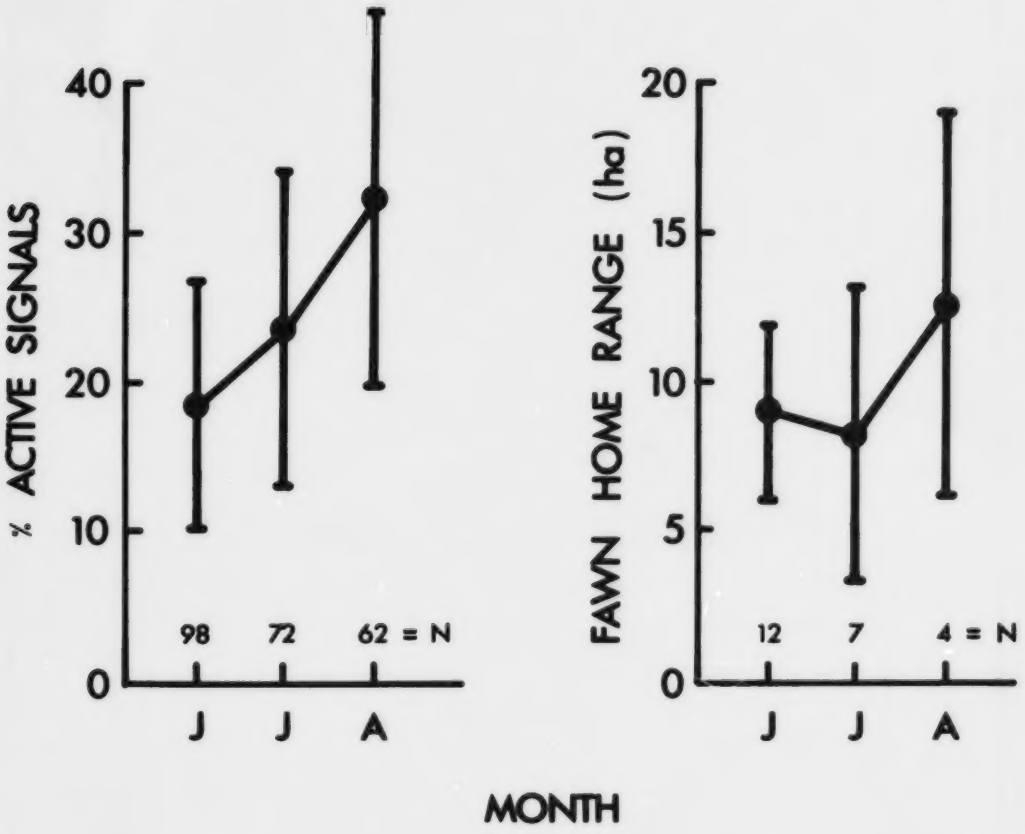

Figure 18. Relationship between summer fawn activity and the size of natal home range (1981). Vertical bars represent 95% CI. Sample sizes are shown above each month (i.e. 98 refers to 98 radio-locations, 12 refers to 12 home ranges).

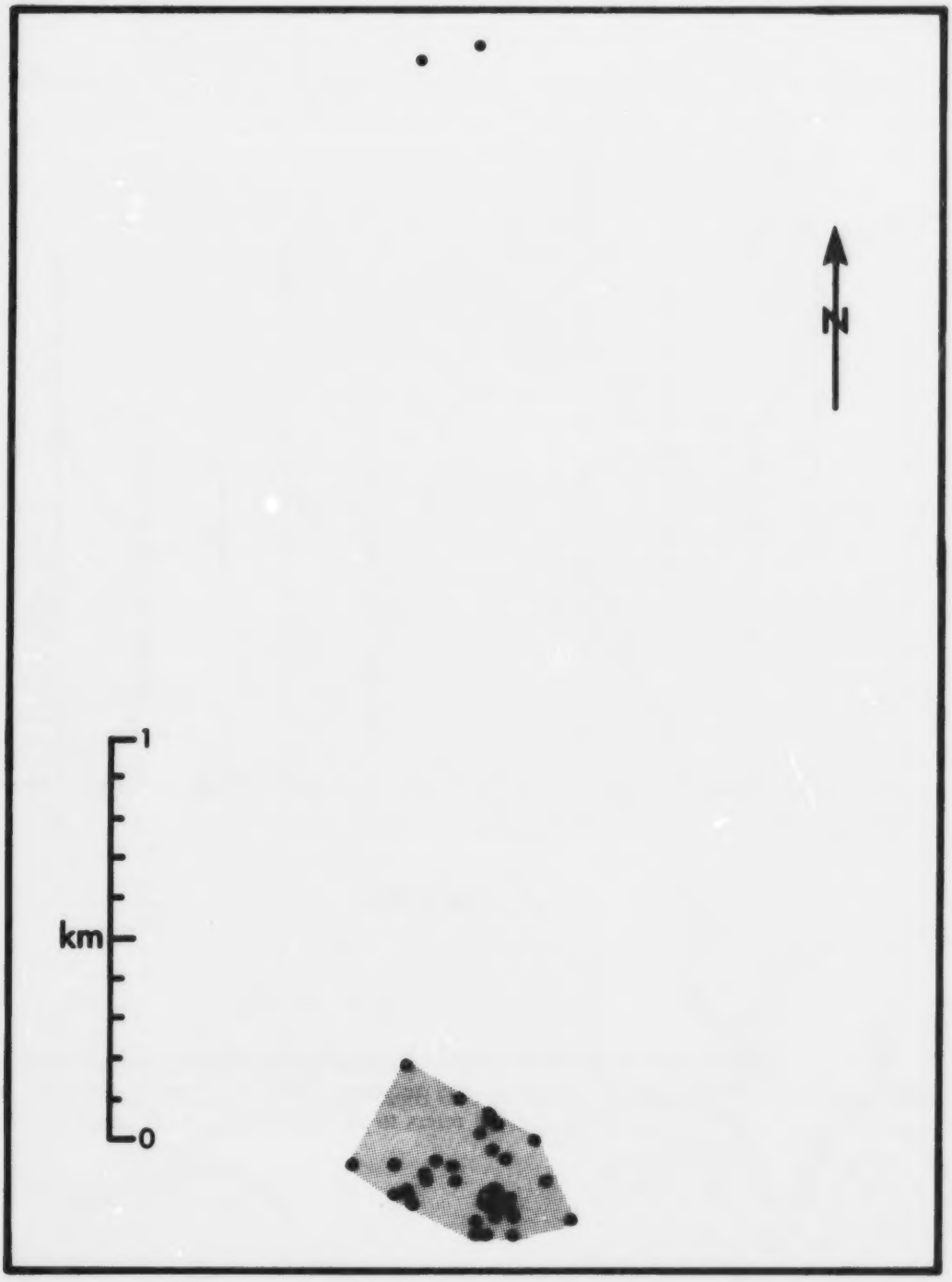

Figure 19. Long range movements by FN 0981(2)-81 during June to August.

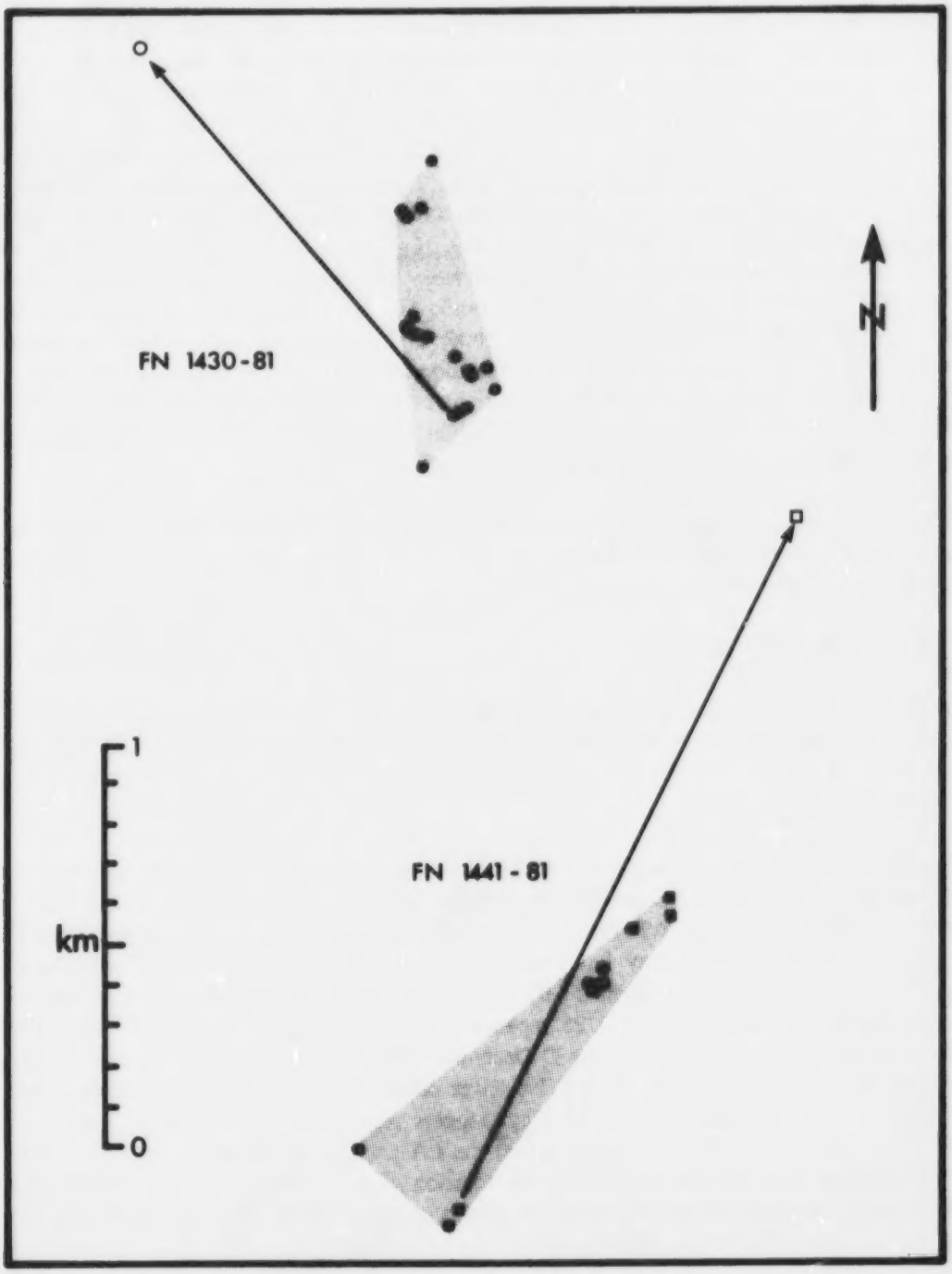

Figure 20. Relationship between radio locations (solid symbols) and carcass locations (open symbols) for two fawns. Arrow shows distance between last radio location and carcass location.

Two fawns monitored throughout the year showed extensive overlap in their seasonal home ranges indicating they were resident as opposed to migratory deer (Fig. 21, Cf. Harestad 1979). To determine if most of the deer were primarily residents, night counts were used to index the seasonal use of cutovers from March until October. As reported by Harestad (1979) for the Nimpkish Valley, deer/km was highest in April and May when deer were concentrated on spring ranges and lower and relatively more stable from June through August when deer were more dispersed on summer ranges (Fig. 22). Harestad (1979) showed that for migratory deer, night counts on high elevation summer ranges increase from spring to summer, while counts on low elevation spring ranges decrease as deer move between low and high elevation habitat. I hypothesized that if deer were primarily resident, there should also be a strong positive correlation between night counts on individual transects between spring and summer, as well as between consecutive summers. Figure 23 shows a significant correlation between spring and summer night counts ($r=.74$, $df=12$, $.002<p<.005$), and for summer night counts between 1980 and 1981 ($r=.78$, $df=12$, $p=.001$). Information on fawn home ranges and night counts support the contention that the Adam River population was composed primarily of resident deer.

Figure 22 indicates a decline in the summer deer/km index in 1981 from 1980 ($t = 4.20$, $df = 16$, $p<.001$), which is consistent with annual declines in the spring night counts documented by the B.C. Fish and Wildlife Branch (Appendix H).

4.4. Wolf Pack Home Ranges

From 28 May to 28 August 1980, six wolves were captured in the Adam and four radio-collared. One pup was captured twice (28 May, 20 July) and another pup, trapped on 22 July, was ear tagged only. Table 6 summarizes the capture information. The radio-tagged wolves were located 454 times (Fig. 24).

Relocations of radio-tagged wolves, elicited howling responses, and scat transects enabled identification of two packs, as previously reported by Scott (1979). Three of the four tagged wolves (WF 0965, WF 0925, WF 1182) were originally members of the UA (Upper Adam) pack. The fourth wolf (WF 1083) may have been a member of the LA (Lower Adam) pack when captured, but this was not confirmed. By 13 January 1981 it became apparent that he was travelling alone (Appendix G). WF 0925 separated from the UA pack during November 1980, but briefly re-associated with the pack from 30 December 1980 to 4 January 1981. It then established a new home range in the lower Adam and Eve River drainage. I was only able to observe WF 0925 with another wolf once on 12 June 1981, but loggers reported seeing it with at least two others during May 1981. Thus WF 0925 either joined the LA pack or established a new pack. This pack was still referred to as the LA pack since the location of the territory was very similar to that of the 1978 pack studied by Scott (1979). Home ranges of pack wolves are shown in Figure 25.

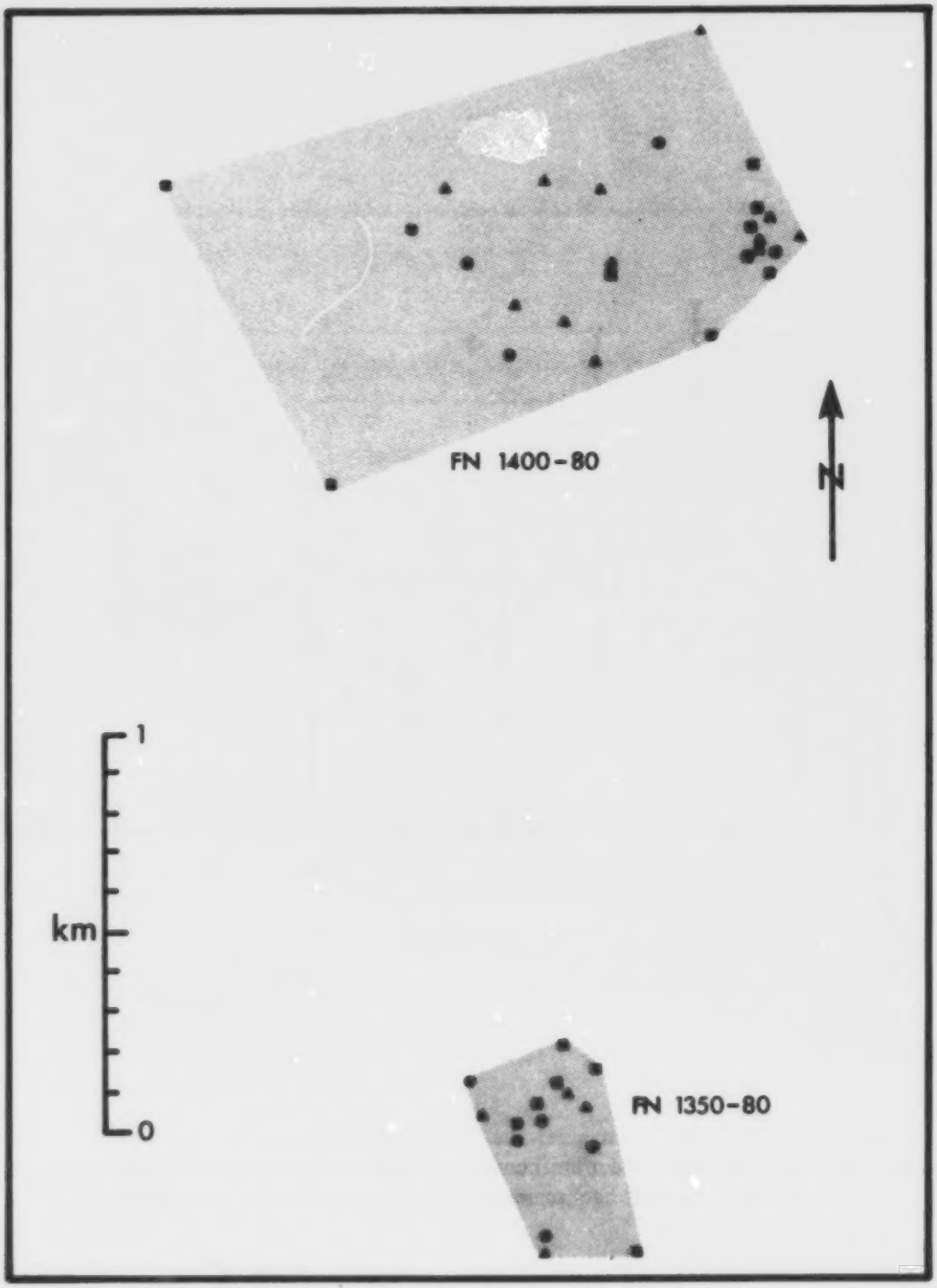

Figure 21. Annual home ranges of FN 1400-81 and FN 1350-80. Summer(●), winter(■), and spring(▲) locations are shown.

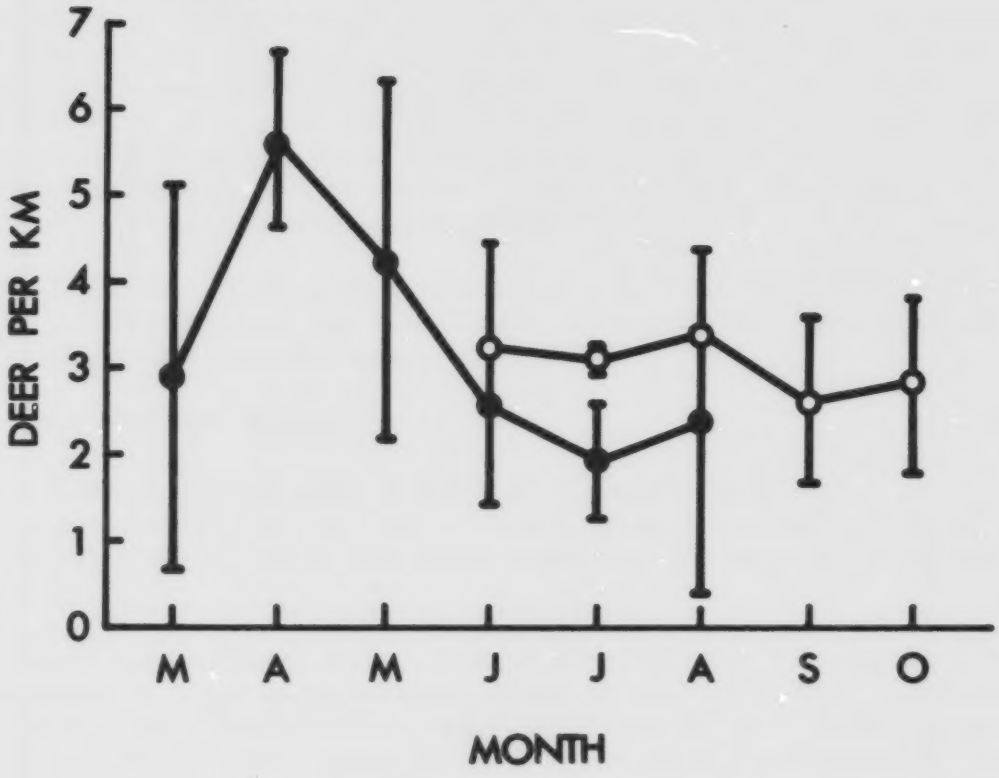

Figure 22. Mean number of deer/km counted at night along road transects in 1980 (○) and 1981 (●). Vertical bars represent 95% CI. Total no. of km = 35.5.

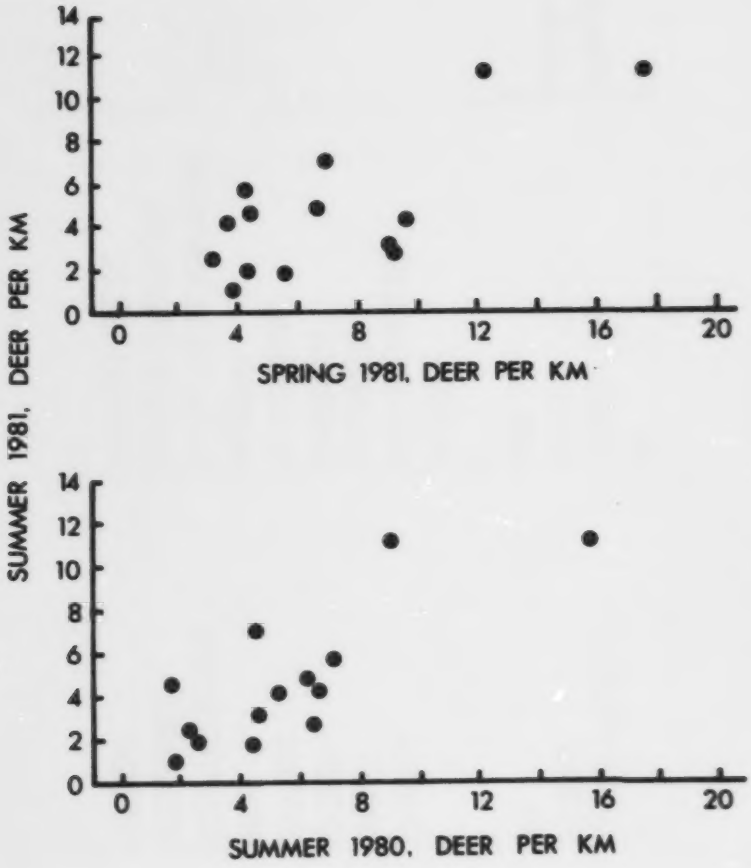

Figure 23. Relationship between: (a) summer and spring night counts, 1981 and; (b) summer 1981 and summer 1980 night counts. Each point represents the peak count for transects >1.0 km in length (n=14 transects).

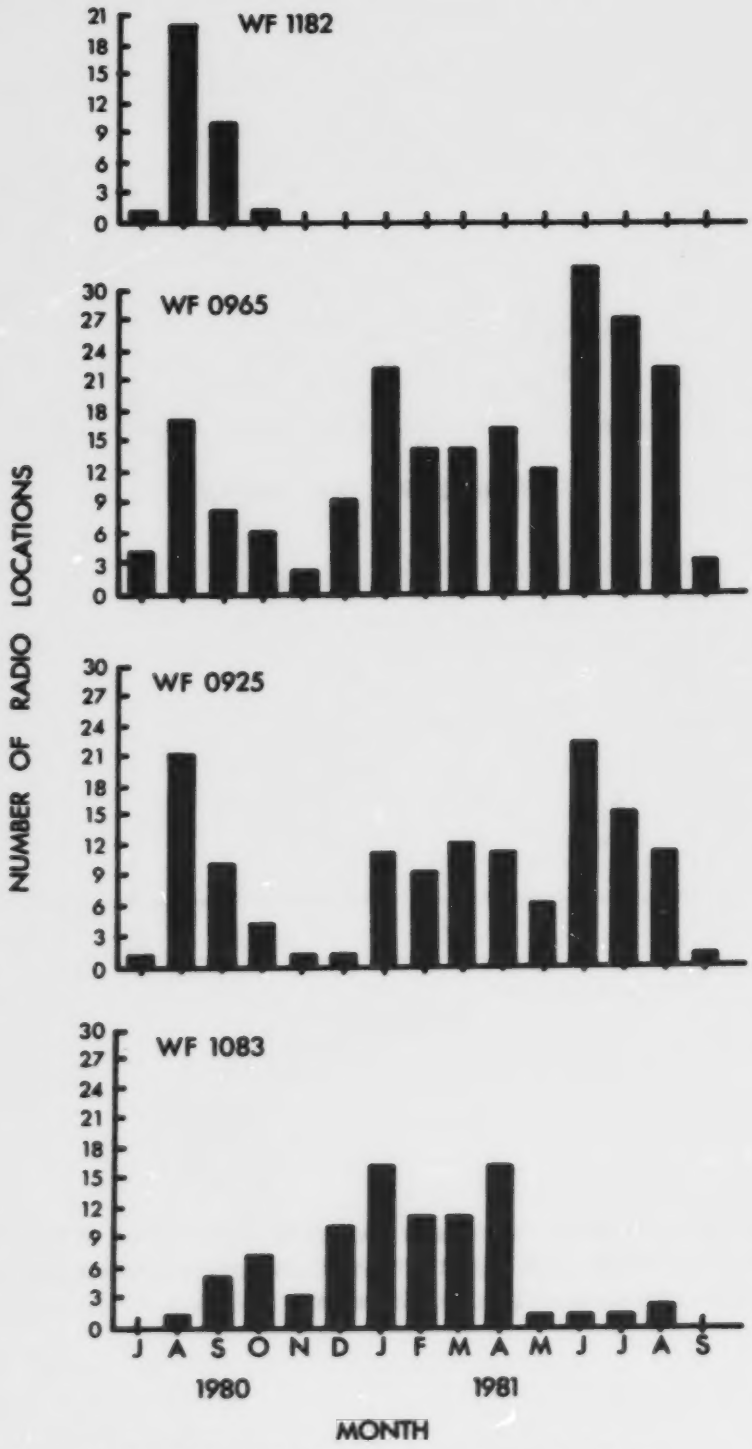

Figure 24. Monthly distribution of radio-locations of tagged wolves.

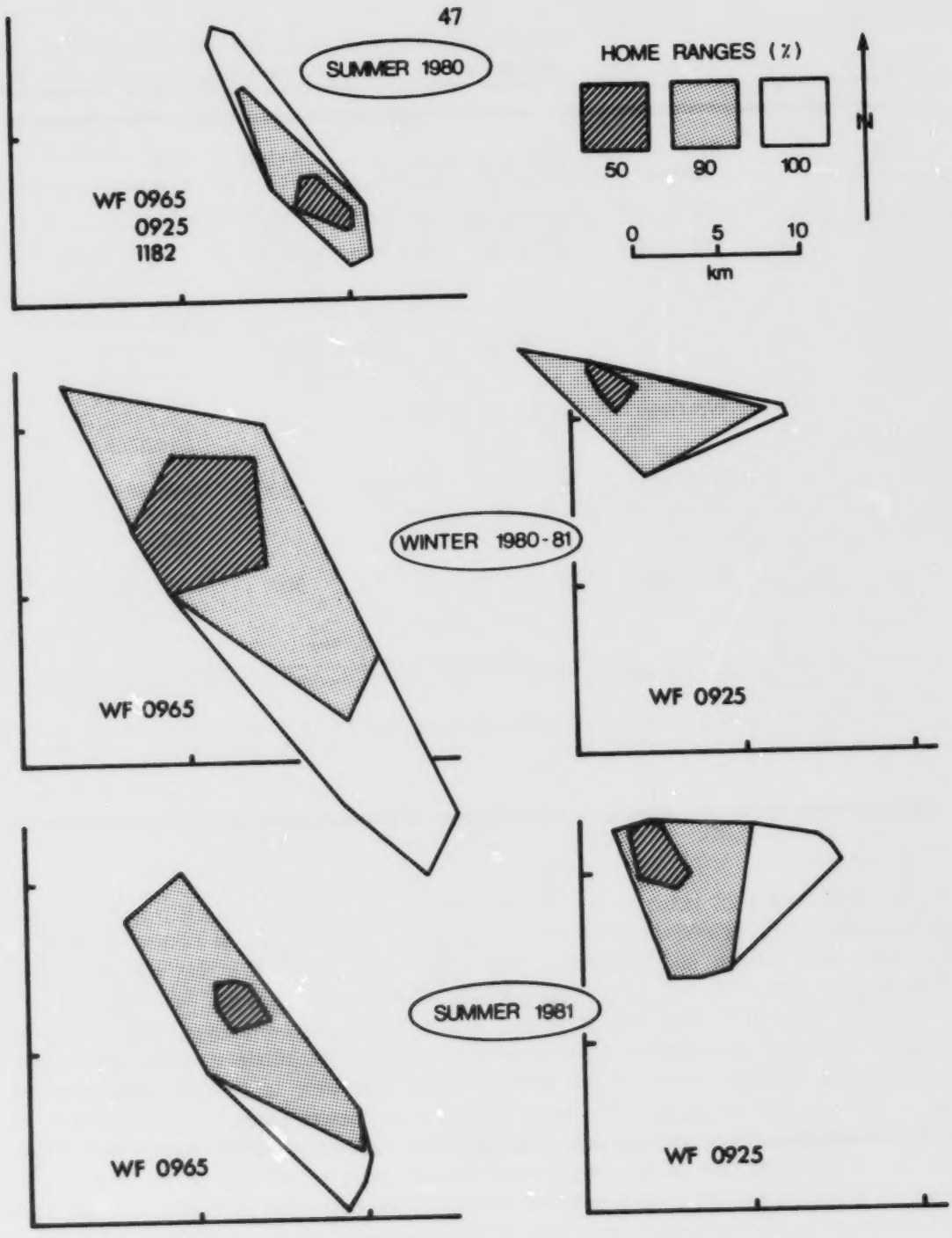

Figure 25. Home ranges of radio-tagged wolves for various periods. Home ranges are scaled for direct comparison between wolves and seasons.

Table 6. Description of wolves captured on the study area between 15 May and 30 August 1980

Pack Affinity	Animal Number	Date Captured	Sex	Age	Weight (kg)	Fate if Known
Upper Adam	WF 1182	28 May 80	M	Pup	5.4	-
	WF 1182	20 Jul 80	M	Pup	16.6	- collar broke off Nov. 80 - shot during winter 80-81
	-	22 Jul 80	-	Pup	-	- run over by vehicle during fall 1981
	WF 0965	22 Jul 80	M	Ad.	32.2	- radio still functioning May 1982
	WF 0925[a]	29 Jul 80	M	Ad.	33.8	- radio still functioning May 1982
Lower Adam	WF 1083[b]	28 Aug 80	M	Ad.	30.8	- dispersed from the study area June 1981

[a] Disassociated with UA pack around 5 January 1981, thereafter considered part of the LA pack (see text).

[b] Thought to be a LA pack wolf when captured, but by 13 January 1981, it was evident that WF 1083 was travelling alone.

Summer 100% wolf pack home ranges (territories) varied from 44 km^2 in 1980 to 83-112 km^2 in 1981 (Table 7). Although 92 locations were obtained for the UA pack in summer 1980, 93% of these were from August and September. The 100% home range size was therefore probably underestimated and 50% and 90% home ranges biased. Scat transects also showed a poor separation of 50% and 50-90% areas (Fig. 26). Scat transects, however, suggested that radio-locations of WF 0965 and WF 0925 during summer 1981 were good approximations of the UA and LA pack territories. Summer territories partially overlapped and were larger than those reported by Scott (1979) in 1978 but smaller than those reported in Minnesota (range = 117 - 132 km^2, Mech 1977a). Although radio-tagged wolves spent relatively little time in the buffer zone (13% of locations of WF 0965, 6% of WF 0925), scat densities were higher than in the 90-100% home ranges of either pack (0.51 $\pm$ 0.15 scats/km/month). Since defecation is a kind of scent-marking and scent-marking increases along the edges of wolf territories (Peters and Mech 1975), it seems likely that scats from both packs were involved.

Table 7. Wolf pack size, pup production, and wolf densities

Area	1978-79[a]		1980-81		1981-82	
	summer	winter	summer	winter	summer	winter
Upper Adam Pack:						
No. of Wolves	10[b]	6-9	8	3-4	8	-
Adults	4	-	4	-	3[c]	-
Pups	4	-	4	-	5	-
Home Range (km^2)						
50%	4	-	7	51	72	-
90%	44	-	29	171	91	-
100%	64	-	44[d]	240	112	-
No. locations	135	-	92	68	110	-
Density (km^2/wolf)[e]	6	-	6[d]	68	14	-
Lower Adam Pack:						
No. of Wolves	5	-	6	1-3	2-3	-
Adults	2	-	3	-	2-3	-
Pups	3	-	3	-	0	-
Home Range (km^2)						
50%	4	-	-	5	10	-
90%	34	-	-	48	57	-
100%	57[f]	-	-	53	83	-
No. locations	213	-	-	24	66	-
Density (km^2/wolf)[e]	11	-	-	27	28	-
Adam River watershed: (351 km^2)						
No. of wolves[g]	21	-	20	-	-	-
Density (km^2/wolf)	17	-	18	-	-	-

[a] from Scott (1979), UA locations from 11 April - 20 November 1978, LA from 10 April - 10 September

[b] 2 wolves unclass., 1 adult male died at capture, 1 shot in fall

[c] 1 wolf found dead on July 8, 1981 near den-site

[d] underestimate of territory size, best estimate based on radio-locations, scat transects and howling responses was 90 km^2; best estimate of wolf density was 11.3 km^2/wolf

[e] wolf density calculated from 100% home range

[f] 1 extreme radio-location resulted in 100% home range = 75.0 km^2, excluding this location territory size was 57.3 km^2

[g] includes estimates for Schoen Lake pack by Hebert *et al.* (1982) in 1978 and by Youds and Stordeur (1981) in 1980. No estimate available in 1981. Lone wolves omitted.

Winter wolf pack territories varied from 53 to 240 km² during 1980-81 (Table 7). Winter movements by WF 1095 and WF 0925 were most extensive during November and December and I was often unable to locate the wolves during this period. Four radio-locations of WF 0965 were in the White River watershed and another seven were in the Eve River watershed. Wolf observations and howling responses during this time period indicated WF 0965 was travelling with the UA pack and scat transects suggested its radio-locations were representative of the pack's movements (Fig. 26). Radio-locations of WF 0925, after permanently dissociating from the UA pack on 5 January 1981, showed extensive overlap with WF 0965. This may have been partially due to the recent splitting of WF 0925 from the UA pack. Scat transects could not be used to verify how representative telemetry locations of WF 0925 were of pack movements due to the overlap of the radio-tagged wolves. Winter territory sizes for the UA pack were comparable to those in Minnesota (range 123 - 183 km², Mech 1977a).

4.5. Wolf Pack Sizes, Composition, and Density

Pack sizes, pup production and wolf densities are shown in Table 7. For comparative purposes, the 1978 information of Scott (1979) is also included. Pack sizes varied little between years, with the exception of the LA pack, which did not appear to produce pups in 1981. The fewer number of wolves estimated during winter is supported by the lower scat densities (summer 1980: 0.63 scats/km/month; winter 1980-81: 0.40 scats/km/month; summer 1981: 0.59 scats/km/month). The reason for the lower wolf density is not known, but human-related mortality and dispersal may have been important (Cf. Scott 1979).

Although summer wolf densities in the study area varied little from 1978-1980, intra-pack wolf densities declined by 57% from 1978 to 1981. This resulted from territorial expansion of the packs since 1978, eliminating the former wolf pack-free zone (Fig. 27).

4.6. Relationship Between Deer Recruitment and Wolf Pack Home Ranges

The small natal home ranges of deer fawns, the resident behaviour of the deer herd, and the relatively large wolf territories indicated that the spatial pattern of fawn survival and recruitment could be analyzed relative to wolf pack home ranges and home sites. It was hypothesized that if wolves were exerting a significant effect on recruitment survival of radio-tagged fawns, August fawn:doe ratios, and spring carryover should be lowest in the 50% home ranges, intermediate in the area between 50% and 90% home ranges, and highest in the area between 90% and 100% boundaries. It was also hypothesized that fawn survival and recruitment should be relatively high in the buffer zone, where wolves spend relatively little time and hunt less (Mech 1977b; Rogers *et al.* 1980).

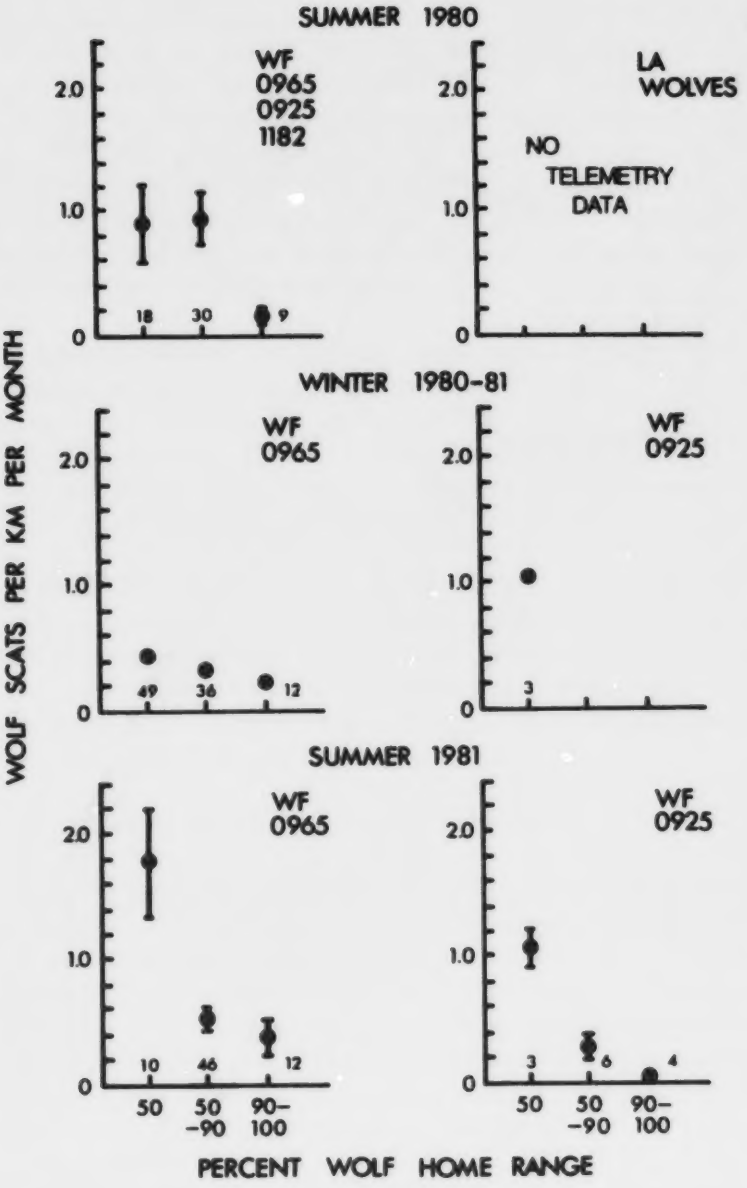

Figure 26. Relationship between mean scat/km/month and home ranges of radio-tagged pack wolves. The 50% home range refers to the area comprised by the 50% home range boundaries, 50-90% is the area enclosed by the 50% and 90% boundaries, and 90-100% is the area enclosed by the 90% and 100% boundaries (see Fig. 25). Vertical bars show ± 1 SE. The no. of km of road sampled is shown above home ranges.

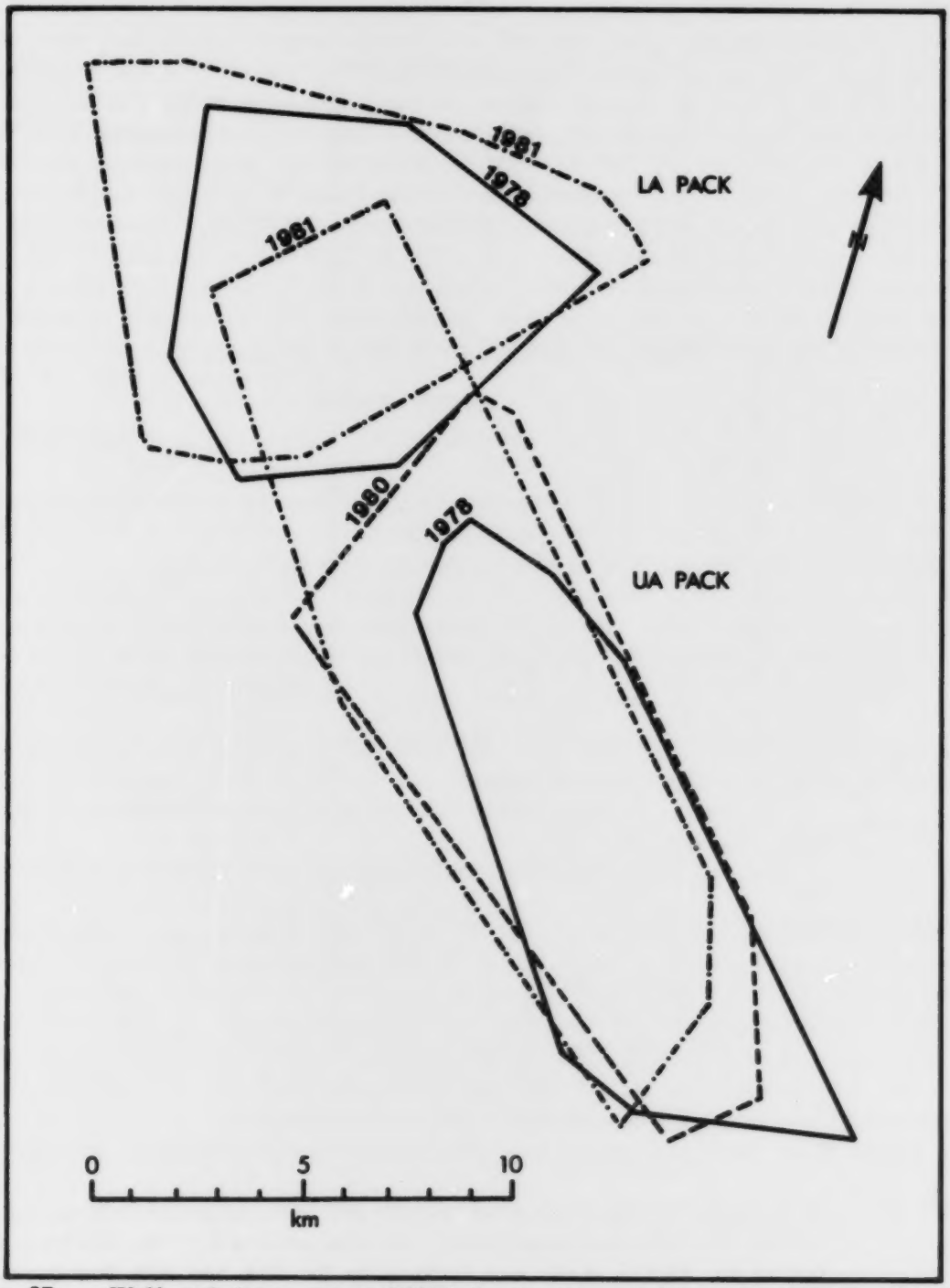

Figure 27. Wolf pack home ranges (100%) for the LA and UA packs, 1978-81. The 1978 home ranges are from Scott (1979). The 1980 home range for the UA pack was estimated (see text).

The spatial relationship between summer survival of radio-tagged fawns and wolf pack home ranges is shown in Figure 28. In 1980, most of the fawns in the vicinity of the UA pack's territory were located either outside or on the edge of the 100% home range boundary where wolf scat transects indicated little wolf activity. Fawn survival was relatively high and only two fawns out of 14 were killed by wolves. In 1981, the distribution of radio-tagged fawns was similar to 1980, but wolf activity was much more concentrated due to the location of home sites. Of five fawns tagged within the 50% home range, four were killed by wolves. An additional two of three fawns tagged just outside the 50% boundary were also killed by wolves. All of these fawns were within 3.2 km (2 mi.) of the UA den and first two rendezvous sites. Thus the spatial patterning of fawn survival appeared to be related to changes in wolf activity.

Fawn:doe ratios within the 50%, 50-90%, and 90-100% home range boundaries of the UA and LA wolves for 1981 are shown in Table 8. Information on wolf territories was too inconclusive to conduct the analysis for 1980. Although the trend shown by the radio-telemetry sample was supported, ratios were not significantly different between boundaries (x^2=3.90, df=3, .25<p<.50), perhaps because of the small sample sizes. There were 34 fawns:100 does outside the 90% home range boundary and 20 fawns:100 does within (x^2=2.94, df=1, .05<p<.10).

A similar relationship existed for spring carryover in 1982 (Table 9). Due to the low classification sample, it was only possible to conduct the analysis relative to the UA pack. Although there was over a 2-fold difference in carryover between the 50% home range and buffer zone these differences were not significant, again probably due to small sample sizes (x^2=3.04, df=2, .10 <p<.25). The analysis, however, does support the contention that wolf-related mortality was most severe during the summer and was not compensated by overwinter fawn losses.

4.7. A Scenario for the Decline of the Adam River Deer Population

A possible scenario for the Adam River deer population decline from 1980 to 1982 is shown in Table 10, based on measured and estimated population parameters. The 18% fawn carryover predicted from the model is the same carryover observed in 1981 and 1982. The predicted fawn:doe ratio in August (46:100) is also close to 44:100 estimated in 1980 but considerably greater than the ratio in 1981 (24:100). Fawn:doe ratios and to a lesser extent, spring carryover, were probably confounded by biases associated with disproportionate deer classification within different portions of the study area. Assuming an annual population decline of 11% from 1980-82, the estimated adult mortality rate was 27%, as opposed to 77% for fawns.

The scenario supports the the hypothesis that low recruitment, resulting from high summer fawn mortality due to wolf predation, was the primary cause of the population declines. The low predation rates during winter is suspect, but may be attributed to the low number of wolves present in the study area during this time.

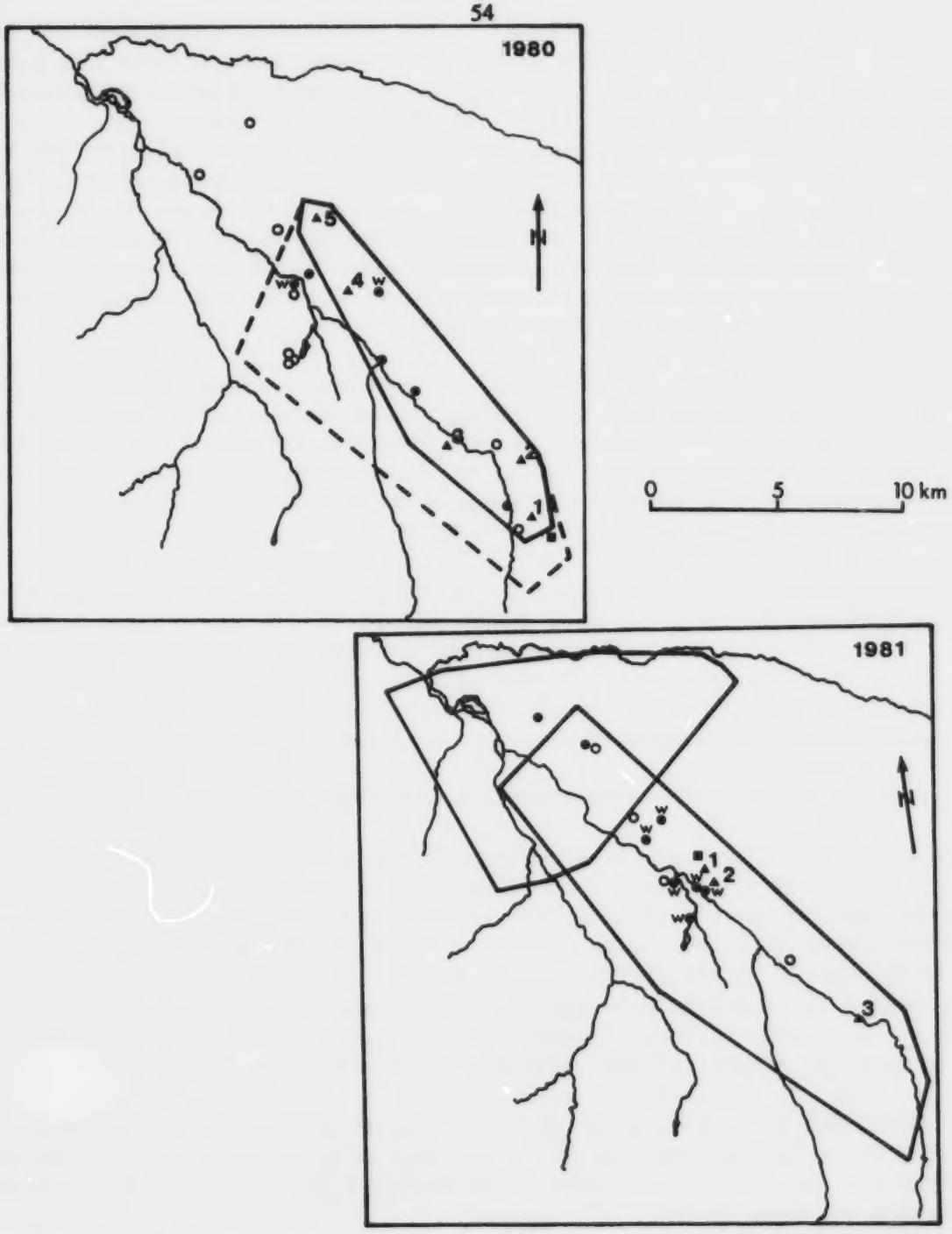

Figure 28. Relationship between survival (○) and mortality (●) of radio- tagged fawns and summer wolf home ranges (100%) during 1980 and 1981. W indicates the fawn was killed by a wolf. Den-sites (■) and rendezvous sites (▲) are shown for the UA pack. The 1980 den-site is the estimated location. Numbers by rendezvous sites indicate order of use during the post-denning period. The dashed line is the adjusted UA wolf territory boundary for 1980.

Table 8. Relationship between August fawn:doe ratios (± 95% CI) and 50%, 90%, and 100% summer wolf pack home ranges (1981)

Home Range[a]	Wolf Pack	Fawns	Does	Fawns: 100 Does	n
50%	UA	9	46	17±11	70
	LA	1	14		
50-90%	UA	21	89	22±10	121
	LA	1	10		
90-100%	UA	2	6	42±31	34
	LA	8	18		
Buffer Zone		12	40	30±19	52

[a] 50% refers to area comprised by 50% home range boundary, 50-90% is the area enclosed by 50 and 90% boundaries and 90-100% is the area enclosed by 90 and 100% boundaries.

Table 9. Relationship between spring carryover (± 95% CI) in 1982, and 50% and 90% summer UA wolf pack home ranges (1981)

Home Range[a]	Fawns	Adults	% Carryover	n
50%	3	25	11±13	28
50-90%	20	95	17± 7	115
Buffer Zone	15	44	25±12	59

[a] 50% refers to area comprised by 50% home range boundary, 50-90% is the area enclosed by 50 and 90% boundaries.

Table 10. A possible scenario for the decline of the Adam deer population, 1980-82

Age Class	Living in June	Dying June to August	Living in Sep.	Dying Sep.-May	Living in June
Adults & Yearlings	100	9[b]	91	18[e]	73-89[g]
Fawns	71[a]	45[c]	26	10[f]	16
Recruitment	(141:100)		(46:100)[d]		(18%)[h]

[a] July-August classified counts indicated 62% does of adults and yearlings. Yearling does = 20% of does. Birth rate = 141 fawns:100 does.

[b] adult and yearling mortality based on fawn:doe ratio in summer wolf diet of 20 adults:-100 fawns, assumes adults die in same proportion observed in scats.

[c] 63% summer q_x is average of 1980-81 radio-tagged fawn mortality estimates.

[d] 46 fawns:100 does in August is close to observed 44 fawns:100 in 1980 but 1.9-fold greater than the 24 fawns:100 does observed in 1981.

[e] adult and yearling mortality calculated by equating observed population decline with projected spring recruitment.

[f] fall (Sep-Nov) fawn mortality rate=13%, winter-spring (Dec-May) mortality calculated as average of 2 rates, based on radio-tagged fawns. The first assumes all missing individuals are dead (q_x=39%), and the second assumes all missing individuals are alive (q_x=19%). Therefore fall-winter-spring estimated mortality = 38%.

[g] observed annual rate of decline from 1980-82 is 11% (i.e., r = (ln Nt - ln No)/t = -.12 where Nt = 4.8 deer/km in 1982 and No = 6.2 deer/km in 1980 and t = 2 years). Annual rate of decline = (1 - antiln r) x 100 = 11.3%.

[h] 18% carryover is same carryover observed in 1981 and 1982.

5. DISCUSSION

5.1 Causes of Low Deer Recruitment on Vancouver Island

A conceptual model of factors affecting recruitment of black-tailed deer on northern Vancouver Island was proposed in Figure 2. Although wolf predation was hypothesized to be limiting recruitment, the model illustrated that predation may only be a proximate mortality factor, mediated indirectly through habitat and/or weather effects ultimately responsible for low fawn production and survival. If this situation was occurring, predation would be partially compensatory, and weather or habitat would be the limiting factor. Alternatively, a combination of factors could be responsible for initiating declines in recruitment with predation sustaining these declines (Mech and Karns 1977; Gasaway *et al.* 1983).

5.1.1. Habitat and weather effects

Numerous predator-prey studies have implicated weather or habitat conditions as the ultimate cause of low juvenile survival in ungulates. In Utah, Beal and Smith (1973) indicated that adverse weather and resulting deteriorated range conditions caused pronghorns (*Antilocapra americana*) to feed in preferred bobcat (*Lynx rufus*) hunting areas where fawns were particularly susceptible. In Texas, Carrol and Brown (1977) documented significant correlations between declining white-tailed deer populations on poor range and fawn survival, even though coyotes were the major proximate mortality factor. In California, Salwasser *et al.* (1978) hypothesized that deteriorating forage conditions on spring migration and early summer habitats affected the nutritional level of the doe during late gestation and was the ultimate cause of low recruitment in a mule deer herd, although coyotes fed heavily on newborn fawns. In Washington, Steigers and Flinders (1980) concluded that intensive removal of coyotes would not substantially reduce mule deer fawn mortality, even though coyotes accounted for 71% of the total mortality, since the fawn population had declined in part due to the loss of critical habitat. In Minnesota, Mech and Karns (1977) found that forest maturation and severe winters precipitated white-tailed deer declines, primarily through reducing productivity and vitality of neonates, and that wolf predation continued these declines. On Isle Royale, the effect of wolf predation on moose calves was also largely mediated through the effects of severe winter weather and poor habitat (Wolfe 1977; Peterson 1977).

In this study, the effects of weather and habitat quality on recruitment was measured indirectly through measuring fetal growth, reproductive rates, physical condition of does and fawns (body weights, CONINDEX), the incidence of disease and parasites, and correlating August fawn:doe ratios with a winter severity index. It was assumed that if either weather or habitat were associated with declines in recruitment, it would be evident from one or more of these indices.

Verme (1965) indicated that the gestation length and hence date of parturition is extended for deer in poor nutritional condition. Verme (1974) also suggested that annual variations in neonatal survival rates quite probably occur because of retarded fetal development following serious malnutrition of pregnant does in winter and early spring. Although fawns may be born alive, they are typically stunted, have decreased viability, and frequently die shortly after birth. Lighter birth

weights have been related to increased neonatal mortality rates in both deer and elk (Verme 1962, 1963, 1977; Thorne *et al.* 1976). Fetal growth and estimated birth dates in this study were comparable to a previous study on Vancouver Island, where wolves were either few or absent (Thomas 1970). Capture weights also seemed comparable to fawns raised by does in captivity maintained on high nutritional diets (Mueller and Sadlier 1980). Thus there was no evidence that fetal viability had been adversely affected.

Where the quality of deer food deteriorates because of high population densities, plant successional changes, or other reasons, one of the most commonly observed results is decreased production of fawns (Cheatum and Severinghaus 1950; Taber 1956; Dahlberg and Guettinger 1956; Teer *et al.* 1965). Thomas (1983) reported that the Northwest Bay population on southern Vancouver Island had reproductive rates comparable to other populations of *O. h. columbianus*, although they are less fecund and obtain their maximum fertility more slowly than most mule deer herds. Fetal rates in the Adam River were comparable to the Northwest Bay population indicating declines in recruitment were not related to reduced productivity.

Both measures of body weight and fat stores have been used to assess physical condition in ungulates. Differences in body weights were related to physical condition by Park and Day (1942), Anderson *et al.* (1972), Kie (1977) and others. Ransom (1965) indicated that the KFI was a suitable indicator of condition in ungulates when FMF remains high, whereas the latter is more indicative of fat reserves at the lower end of the condition scale. Trainer *et al.* (1979) combined both measurements to form a condition index (CONINDEX), which is a more sensitive indicator of body condition than either index alone. Mean age-specific weights of females were comparable to weights from deer herds on northern Vancouver Island prior to the increase in wolves. CONINDEX values of Adam-Eve fawns and does were also comparable to baseline values reported by Trainer *et al.* (1979) for mule deer. Thus deer appeared to be in satisfactory condition during the period of this study.

When food is limiting, poor physiological condition of deer often results in heavy disease and parasite burdens (Klein 1970). Fawns and yearlings characteristically have lower resistance to diseases and parasites than adults (Longhurst 1955). Thirteen of 22 fawns had heavy *E. coli* loads. Since *E. coli* are present in neonates of many domestic ungulate species and certain strains constitute normal flora for deer (Trainer *et al.* 1981; M. Hewitt, pers. comm.), the significance of this bacteria could not be ascertained, but was likely low. Tests for *Salmonella*, a disease of known importance in fawn survival in wild herds (Robinson *et al.* 1970; Cook *et al.* 1971; Daniel 1976) were negative in every case. Disease-related deaths, which may have been nutritionally related, occurred twice, but was not considered a serious mortality factor. The incidence of parasites in fawns was also low. It seems unlikely that disease or parasites could have accounted for declines in fawn recruitment.

Negative correlations between winter severity and recruitment have been demonstrated for most ungulates, including moose (Haber 1977), caribou (*Rangifer tarandus*) (Elliott *et al.*, in prep.), Dall's sheep (*Ovis dalli*) (Murphy and Whitten 1976), elk (Picton and Knight 1971), and mule deer (Picton 1979). A similar relationship was shown for black-tailed deer on southern Vancouver Island from 1954-68 (Smith, no date). A severe winter during 1971- 72 also markedly depressed the

fawn:doe ratio the following summer on northern Vancouver Island (Jones and Mason 1983). No relationship, however, existed between August fawn:doe ratios and winter severity in the Adam River from 1976-81. During the 1980-81 winter, snowfall was extremely low, although August fawn:doe ratios in 1981 were the lowest recorded since 1975. Chilling of neonates, induced by rain, cold temperatures, and wind is not a frequent cause of summer mortality on Vancouver Island (Smith, no date), and also did not appear to be important during this study. It seems doubtful that weather was an important factor in reducing recruitment.

The influence of logging in altering wolf-deer relationships on the Island was not investigated. Bergerud (1981) suggests logging concentrates moose in the remaining forest stands and provides avenues of access via logging roads that increase the speed and effectiveness of search for wolves. On Vancouver Island, Hebert *et al.* (1982) and Harestad (1979) suggested that concentration of deer in residual stands of mature timber during winter or in cutovers during spring could make them more vulnerable to predation, since wolves should concentrate their activities where prey density and foraging efficiency are greatest. Presumably, fawns would be most vulnerable in such situations. Due to a series of mild winters, deer have not concentrated on winter ranges (R. Davies, pers. comm). Concentration on spring ranges, however, could have made deer more vulnerable to predation. Fawns (short-yearlings), remaining on spring ranges after having been chased off by their mothers, may have been exceptionally vulnerable. An examination of three deer kills made by a lone wolf during the spring indicated that two were fawns (the third was unclassified). During summer, radio-tagged fawns tended to reside more in cutovers rather than in forested areas. Regenerating cutovers probably provided effective hiding habitat for fawns since visibility was usually lower than in mature forested habitats. It was also apparent that wolves made extensive use of logging roads in the study area and their search time could have been lower than in unlogged watersheds. A proper assessment of the effects of logging and roads, however, would require measuring fawn mortality rates in both developed and undeveloped watersheds occupied by wolves. Limited inventory, based on annual pellet group counts in unlogged watersheds, indicates deer populations have also declined where wolves are present (Jones and Mason 1983; D. Janz, pers. comm.).

5.1.2. Hunting Effects

Predation effects are usually much more pronounced in heavily as opposed to lightly hunted ungulate populations (Haber 1977; Connolly 1978; Gasaway *et al.* 1983). Bergerud (1980, 1983) implied that a low calf recruitment rate in caribou, maintained by predation, is balanced by a relatively low mortality rate in adults. Hunting, by increasing adult mortality, induces negative annual increments causing subsequent population declines. For other species such as moose and deer, yearlings comprise a larger proportion of the harvest due to their high vulnerability. Although fawns and calves are also vulnerable, they are typically selected against (Maguire and Severinghaus 1954; Simkin 1965; McCullough 1979; Crete *et al.* 1981). Increasing the harvest on fawns or calves is often encouraged, even for declining populations, since killing is concentrated on the age group with the highest death risk in the coming winter, and leaves the more productive component for breeding. However, where wolf predation on juveniles is intensive, fawn/calf harvests may hasten reductions in recruitment and lead to accelerated population declines (Eastman and Hatter, in press).

On Vancouver Island, Smith (1968) indicated that with wolves few or absent, hunters shot proportionately fewer fawns or took them in their proportion in the population. In the Adam-Eve and Nimpkish where wolf densities were high, hunters appeared to select for fawns (this study; Jones and Mason 1983). Fawn selectivity appeared to increase in the Adam-Eve as spring carryover and deer numbers decreased. Although it was not certain why this occurred, it may be that as the herd declined, hunters became more willing to shoot fawns when fewer opportunities were available for larger deer. Although there was no quantitative evidence that fawn hunting had a measurable effect on recruitment, it seems probable that hunting was partially additive to predation. Thus the role of antlerless hunting may have been to initiate declines slightly sooner and perhaps more quickly in the presence of wolf predation.

5.1.3. Predation effects

Several studies have implicated wolf predation as the primary factor limiting juvenile recruitment in ungulate populations. In a study of the Kaminuriak barren-ground caribou, Miller and Broughton (1974) found that wolves killed 18 of 57 newborn calves, and concluded wolf predation was the principal cause of mortality during both the calving and post-calving periods. Bergerud (1980, 1983) argued that low caribou calf recruitment rates for many North American herds result from predation, primarily by wolves. Gasaway *et al.* (1983) showed negative correlations for both caribou and moose calf recruitment, with wolf numbers in interior Alaska, as did Bergerud *et al.* (1983) for moose calf recruitment on Isle Royale. Other studies showed bears to be effective predators on neonatal ungulates. Schlegel (1976) found that among 67 radio-tagged elk calves in north central Idaho, 68% died by the end of October with black bear predation responsible for 94% of the mortality. Franzmann *et al.* (1980) identified black bears as the major cause of moose calf mortality on the Kenai Peninsula in Alaska, accounting for 59% of the mortality from a sample of 47 radio-tagged moose. Ballard *et al.* (1981) found that predation by brown bears accounted for 79% of the mortality of 123 radio- tagged moose calves in south central Alaska. Bergerud and Butler (1978), working in northern British Columbia on caribou, and D. Larson (pers. comm.) working in the Yukon on moose, suggested grizzly bears are important predators on the calving grounds and that wolves are important predators during the post calving period. Cougars can also be important predators on ungulates (Robinette *et al.* 1959; Homocker 1976; Nellis 1977). An important component of these studies was that much of the predator-involved juvenile mortality occurred within the first 2-3 months of life, which in some cases was capable of limiting population growth. Allee *et al.* (1949) noted that predation is frequently directed against the immature stages of the prey and as such may constitute an effective limiting factor.

Similarly, in this study, predation appeared to be the major mortality factor limiting black-tailed deer recruitment, with most of the predation attributed to wolves. Two-thirds of the summer fawn mortality was traced to wolves, whereas only one radio-tagged fawn was killed by a bear and none by cougars. The high mortality rate of radio-tagged fawns in June and July, followed by a reduced mortality rate in August, was supported by the frequency of occurrence of fawns in the wolves' diet during this period. Collared fawns closer to the UA wolf den site had a higher mortality rate than fawns further away. August fawn:doe ratios and spring carryover showed an inverse relation-

ship to wolf activity with recruitment lowest in areas most frequently used by wolves. In the Nimpkish Valley, Jones and Mason (1983) showed that fawns:100 does in summer and carryover in spring were negatively correlated with a wolf index. An experimental wolf control program in the Nimpkish Valley found that August fawn:doe ratios increased from 21 fawns:100 does in 1982 to 53 fawns:100 does in 1983, following wolf reduction in 1982-83. The Adam-Eve, with no wolf control, declined to 11 fawns:100 does in 1983 (Atkinson and Janz 1983). The high wolf densities, small size of black-tailed deer, and relatively low availability and use of alternate prey appear to be important factors contributing to low recruitment. Hebert *et al.* (1982) suggested that the three wolf packs in the Adam River watershed in 1978 could have utilized 400-600 deer annually, depending on the percentage of fawns in the diet.

5.2. Management Options for the Vancouver Island Wolf-Deer System

Information presented here and elsewhere (Hebert 1981; Hebert *et al.* 1982; Hatter 1982; Atkinson and Janz 1983; Jones and Mason 1983) favour the hypothesis that wolf predation is presently controlling deer populations on northern Vancouver Island. Recent inventories (1976-83) indicate that the Adam-Eve herd, as well as other northern herds, have followed a reverse sigmoid growth curve with continued depressed recruitment, and only a slight reduction in wolf densities (Appendix H). That wolves may continue to suppress deer numbers for several more years is suggested from observations of a coastal wolf-deer system in southeastern Alaska. In that system, following a major deer decline, initiated by weather and continued by predation, a lag of approximately 5 years occurred before wolf densities declined to sufficiently low levels to allow deer numbers to once again increase (Olson 1979; Klein 1981).

Given the high probability of a protracted deer recovery, wolf predation poses a serious problem to meeting both deer and wolf management objectives (Hatter and Janz 1983). Gasaway *et al.* (1983) indicated that managers have three options when predation limits the growth of ungulate populations: (1) wait for a more or less natural change of events; (2) reduce or eliminate harvest by man during critical periods for prey populations; or (3) hasten the increase in prey by reducing wolves. Option 1 is not advisable in key deer production areas on Vancouver Island, managed for high sustained yields, due to the lengthy period that may be required (B.C. Ministry of Environment 1980). At present, option 2 offers little hope since wolves appear to have sufficient control over the deer population to maintain the decline in the absence of hunting. Unless deer recruitment increases, eliminating hunting would seem to have very little effect. Option 3, through artificial reduction of wolf numbers, in conjunction with a reduction in the hunter harvest, appears to be the most viable management option for quickly increasing deer populations. Wolf control, to maintain another wildlife (prey) population at a desired level, is considered a valid wolf management objective in British Columbia (B.C. Ministry of Environment 1979). Jones and Mason (1983) indicated that high deer populations on northern Vancouver Island are used to justify deferral of important winter ranges from logging. At present low deer populations have reduced this justification. Wolf control can therefore serve in the interest of maintaining both viable wolf and deer populations.

5.2.1. A proposal for wolf control

Deliberate attempts to perturbate the wolf-deer system through wolf control can provide considerably more information about the system's dynamics than presently known, if coupled with an intensive monitoring program. Such an "adaptive management" approach allows learning to take place as management proceeds (Holling 1978). It has been used successfully in fisheries to enhance management efforts, but until recently has received little attention in wildlife management (Page 1983). The following proposal for wolf control is designed with this in mind, i.e. active management of wolves to attempt to increase deer populations and hunter harvests, while also increasing understanding of the inter-relationships between wolves, deer and hunting. A key consideration to the wolf control proposal is maintenance of a viable wolf population.

Keith (1983) provided the following simple numerical model to predict the interaction between deer numbers, wolf predation, and hunting:

$$N = \frac{K}{(\lambda-1)(1-H)}$$

where N = deer numbers per wolf in spring before births
λ = potential finite rate of increase of deer
H = proportion of the annual increment of deer removed by hunting
K = number of deer killed per wolf annually

This assumes that hunting mortality and wolf predation are largely additive. The model can also be used to calculate initial reductions in the wolf population necessary to stimulate different rates of increase in deer, providing a stable deer:wolf ratio has developed and the net annual increment to the deer population is zero. Under these conditions wolf control can act to reduce wolf numbers, and by maintaining the resulting deer:wolf ratio, enable wolves, deer, and hunter harvests to increase.

Information has been presented to suggest wolves and deer may be tracking a low equilibrium condition on northern Vancouver Island. Hence the necessary conditions to implement the model may be satisfied, at least for some watersheds. Parameter estimates for the model can also be approximated from present information. The potential finite rate of increase of deer on the Island is in excess of $\lambda = 1.4$, as the Nanaimo River population reached this growth rate from 1976-79 (B.C. Fish and Wildlife Branch, unpubl.). Assuming some density dependence in deer population growth rates and occasional moderate to severe winters, long term (up to 10 years) sustained rates of increase from low densities in the absence of predation and hunting could average $\lambda = 1.3$. The proportion of the annual increment of deer removed by hunting varies markedly for different herds, but probably ranges from 20 to 60% (ESSA 1979). The number of deer killed per wolf annually has been estimated at 20 to 30 deer/wolf/year, based on scat analysis and extrapolation of food consumption rates reported in the literature (Hebert *et al.* 1982).

Figure 29 indicates the tradeoffs expected between level of wolf reduction, the time allotted for a deer population to double in size (a measure of its rate of increase), and the proportion of the annual increment removed by hunting, based on the wolf control model. The value of K does not influence the rate of increase of deer, providing it remains constant over the observed range of deer densities. As an example, if the hunter harvest removed 20% of the annual increment and the wolf population was initially reduced by 30%, 10 years would be required for the deer population to double in size. If the wolf population was reduced by 80%, only 4 years would be required. Elimination of the antlerless harvest should also increase λ and reduce the recovery time (Cf. Bergerud 1971).

It is recommended that the wolf control model be evaluated further as a hypothesis to attempt to understand and predict the behaviour of the wolf-deer system resulting from wolf control. A crude approximation to obtaining desired wolf reductions in specific watersheds can be made by reducing wolf population indices correspondingly (e.g. wolf sighting index, wolf scat transects). Deer population responses can be measured from changes in recruitment rates and annual night counts. As deer numbers increase, wolf numbers should be allowed to slowly increase to maintain a constant deer:wolf ratio. Subsequent control efforts to stabilize the deer:wolf ratio will provide the information on how quickly wolf numbers respond to increases in deer density. By maintaining and monitoring control areas, the cost- effectiveness of wolf control can also be evaluated. Since the system may be considerably more complex than predicted, conditions should be monitored closely to falsify incorrect assumptions and explicitly define functional relationships (e.g. functional and numerical responses of wolves). As understanding improves, realism can be increased with more complex interactions with weather, habitat, and alternate prey incorporated.

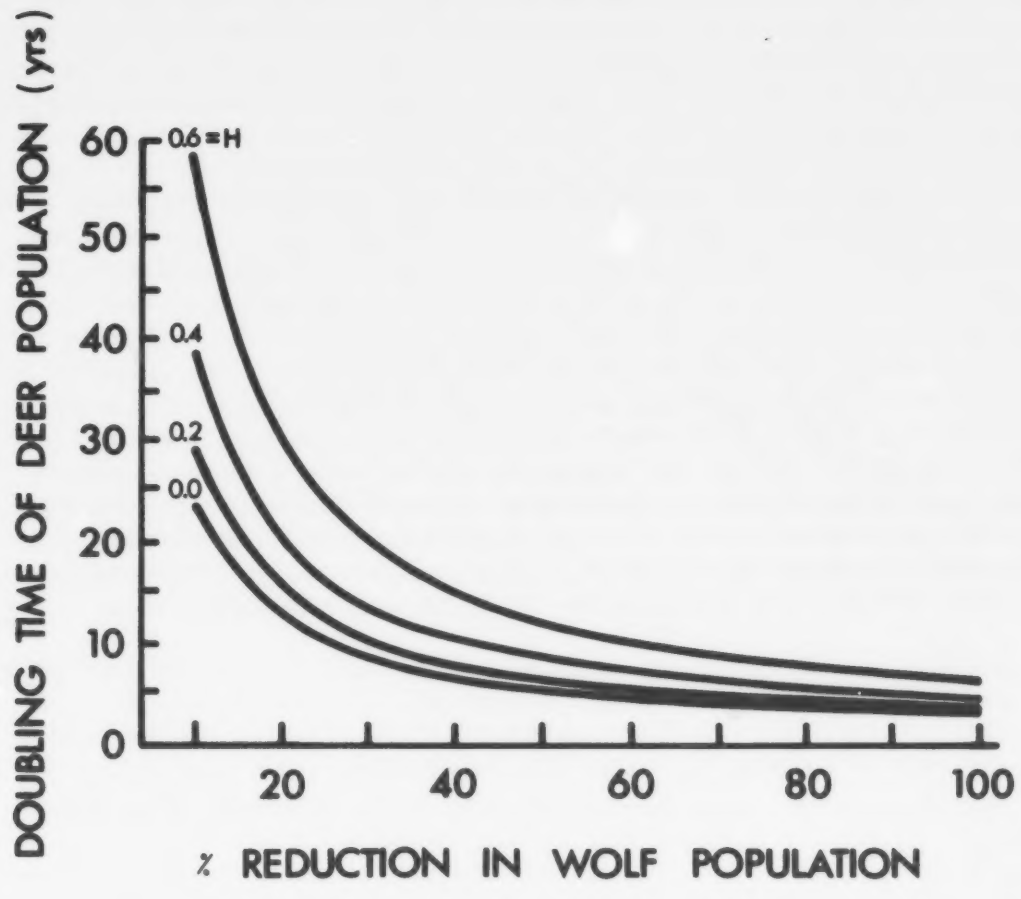

Figure 29. Rate of recovery of a hypothetical deer population with a potential finite rate of increase of $\lambda = 1.30$. Several hunting rates and different initial reductions in the wolf population from a stationary deer:wolf ratio are shown. Rate of recovery is expressed as doubling time or the number of years required for a deer herd to increase two times in size. H refers to the proportion of the annual increment to the deer herd removed by hunting (see text).

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APPENDIX A. Form used to describe fawn at capture.

APPENDIX B. Forms used to describe deer fawn mortality (modified from Ballard and Taylor 1978)

DEER FAWN COLLARING FORM

FAWN NO. _____ DATE _____ TIME CAUGHT _____ RELEASED _____

COLLAR NO. _____ RADIO FREQUENCY _____ MAGNET REMOVED: YES _____

EAR TAG: R _____ L _____

LOCATION _____

ELEV _____ SLOPE _____ ASPECT _____

VEGETATION TYPE _____

SEX _____ WT _____ EST. AGE _____

BLOOD: YES _____ NO _____ RECTAL SWAB: YES _____ NO _____

MOISTURE OF HAIR: WET _____ DRY _____ MATTED _____

DAMPNESS IN EARS _____

NAVAL: BLOODY _____ MOIST _____ DRY _____

HOOVES: ENTIRELY SOFT _____ LESS THAN 1/2 HARDENED _____

ALL HARDENED _____

RAGGED: YES _____ NO _____

GRASS STAINED: YES _____ NO _____

DEW CLAWS: SOFT _____ HARD _____

STATURE & STABILITY

INSECURE AND WOBBLY: YES _____ NO _____

LEGS SPREAD: YES _____ NO _____

HUMPED POSTURE WHEN STANDING: YES _____ NO _____

GENERAL COMMENTS (HOW CAPTURED, HOW DOE, FAWN REACTED)

_____

_____

_____

DEER FAWN MORTALITY FORM

FAWN NUMBER _____ DATE & TIME _____ DATE CAPTURED _____

KILL LOCATION _____ HOW LONG DEAD _____

APPROX. AGE OF FAWN _____ LAST MONITORED: DATE _____ TIME _____

PHOTOS _____ CARCASS WEIGHT _____ INCISOR LENGTH _____

HIND LEG LENGTH _____ HEART GIRTH _____ TOTAL LENGTH _____

DESCRIPTION OF KILL SITE: SLOPE _____ ASPECT _____ VEGETATION _____

CANOPY COVER _____ % ELEV _____ NEAREST ROAD _____

COMMENTS:

DESCRIPTION OF CARCASS: AMOUNT CONSUMED _____ % DISTANCE FROM KILL SITE _____

TONGUE REMOVED: YES ____ NO ____ EARS REMOVED: YES ____ NO ____

COLLAR REMOVED: YES ____ NO ____ HIDE INVERTED: YES ____ NO ____

EYES REMOVED: YES ____ NO ____ SUBSUTANEOUS HEMORRHAGE: YES ____ NO ____

CLAW MARKS ON HIDE: YES ____ NO ____ LOCATION _____

PUNCTURE WOUNDS: YES ____ NO ____ DIAMETER: _____

LOCATION: _____

COMMENTS:

PREDATOR SIGN: SCATS NEAR CARCASS: YES ____ NO ____ HOW MANY: ____ SPECIES _____

SCAT COLLECTED: YES ____ NO ____ CARCASS COVERED: YES ____ NO ____ MATERIAL _____

TRACKS NEAR CARCASS: YES ____ NO ____ SPECIES _____

HAIR NEAR CARCASS: YES ____ NO ____ SPECIES _____

TRACK MEASUREMENTS: _____

COMMENTS:

APPENDIX C. Summary of deer composition in the Adam-Eve, 1980-82.

A. Summer Counts

Year	Month	Males		Females	Fawns	U/C Adults	U/C
		Adults	Yrlgs				
1980	June	<-------67------->		107	15	44	0
	July	97	45	208	63	30	18
	August	80	38	192	85	34	6
1981	June	<------147------->		184	16	140	0
	July	90	46	229	36	45	5
	August	94	46	243	58	34	5

B. Spring Counts

Year	Month	Adults	Fawns	U/C
1981	April	462	98	6
1982	May	169	38	24

APPENDIX D. Morphological measurements and condition indices from deer collected in spring, 1980 and 1981.

Measurements	Fawn			Female			Male		
(cm or kg)	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Whole wt.	26.3	4.0	8	45.7	7.2	14	39.5	-	1
Eviscerated wt.	19.5	3.2	8	31.1	5.0	14	29.5	-	1
Total length	123.3	11.3	8	137.0	9.7	14	132.0	-	1
Chest girth	66.6	3.4	8	80.5	6.1	14	81.5	-	1
Hind foot	38.7	1.4	8	41.1	1.6	14	43.2	-	1
Femur marrow fat	42.2	26.1	9	70.3	17.4	14	63.8	24.5	5
Kidney fat index	12.6	6.1	7	19.7	12.2	14	16.0	5.7	4
CONINDEX	42.9	26.8	9	66.1	27.3	14	68.3	17.1	5

APPENDIX E. Summary of radio-telemetry for 26 fawns, summer 1980 and 1981.

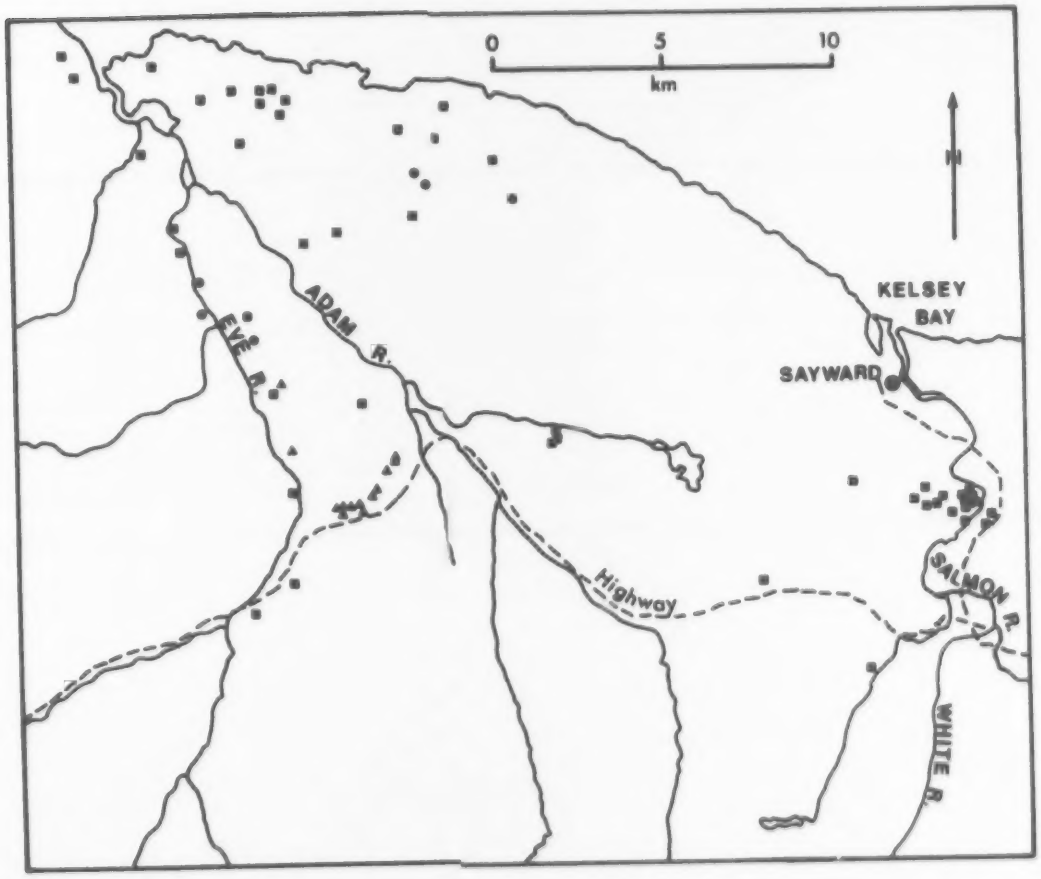
Fawn No.	Sex	Wt. (kg)	Date Captured	Last Date Monitored	No. Radio-days	Fate
1980						
6551	F	1.8	20 Jun	20 Jun	1	accident
6328#2	M	1.7	7 Jul	19 Jul	13	disease
6553	F	2.8	11 Jun	20 Dec	193	collar off
6554	M	3.0	12 Jun	31 Aug	81	wolf
6555	M	4.2	17 Jun	22 Apr	310	starved
6556	F	2.2	5 Jun	8 Jul	34	collar off
6557	F	2.8	19 Jun	31 May	347	collar off
6558	F	3.2	18 Jun	21 Aug	65	lost signal
6559	F	34.9	19 Jun	21 Jun	3	bear
6560	M	3.8	19 Jun	10 Nov	145	shot
6326	M	3.8	19 Jun	3 Jul	15	disease
6327	F	2.8	7 Jun	31 Aug	86	collar off
6328	F	3.2	13 Jun	27 Jun	15	wolf
6329	F	4.3	20 Jun	14 Oct	117	collar off
6330	F	3.6	22 Jun	13 Jan	206	collar off
1981						
6556	M	3.7	9 Jun	30 Jul	53	wolf
6329	F	2.6	9 Jun	25 Jun	17	wolf
6559	M	1.8	10 Jun	18 Jul	39	wolf
6326	M	3.5	14 Jun	5 Jul	22	wolf
6330	M	3.0	14 Jun	4 Jul	21	wolf
6554	F	2.8	18 Jun	15 Nov	151	alive
6328	F	3.0	18 Jun	21 Jun	4	accident
6553	F	1.7	19 Jun	15 Nov	150	alive
6327	M	3.7	20 Jun	30 Aug	72	lost signal
6560	F	4.2	21 Jun	8 Jul	18	wolf
6329#2	F	5.3	29 Jun	30 Jun	2	lost signal
6328#2	F	4.8	25 Jun	15 Nov	144	alive
6330#2	M	4.2	11 Jul	13 Jul	3	disease

APPENDIX F. Summary of home-range data for 16 fawns, summer 1980 and 1981.

Fawn No.	Year	Radio-telemetry Period	No. of Radio-locations	Home Range in ha
0950	1980	7 Jun - 31 Aug	4	.6
1160	1980	22 Jun - 22 Aug	3	9.1
1250	1980	11 Jun - 8 Aug	5	7.6
1370	1980	5 Jun - 8 Aug	5	19.6
0950	1981	20 Jun - 28 Aug	38	34.2
0980	1981	18 Jun - 21 Jun	3	.3
0981(2)	1981	25 Jun - 28 Aug	43	13.7
1120	1981	9 Jun - 23 Jun	5	1.8
0900	1981	14 Jun - 29 Jun	10	9.7
1160	1981	14 Jun - 29 Jun	10	6.5
1160(2)	1981	11 Jul - 13 Jul	3	.6
1251	1981	19 Jun - 28 Aug	40	31.5
1441	1981	21 Jun - 29 Jun	10	15.5
1280	1981	18 Jun - 29 Aug	37	15.7
1370	1981	9 Jun - 28 Jul	20	71.0
1430	1981	10 Jun - 17 Jul	18	10.6

APPENDIX G. Radio-locations of the lone wolf (WF 1083) from 28 August 1980 to 1 May 1981. From 28 August 1980 to 6 January, 1981, the wolf remained in the lower Adam-Eve river area. On 13 January 1981, he was located in the White River watershed and from 15 January to 12 February he resided in the lower Salmon River valley, in an area of about 4.7 km². Locations between 24 February and 17 March indicated he had returned to the lower Adam-Eve area, but on 24 March he was located again in the Salmon River area and remained there until 28 March. On 29 March he moved back into the study area and from 16 April until 1 May was consistently located in a 1.3 km² area west of Rooney Lake. From 16 to 21 April, I located 3 deer kills (2 fawns, 1 U/C) of which WF 1083 was observed at two of them. I lost contact with the wolf until 24 June when he was relocated by aircraft 5 km north of Menzies Bay, approximately 60 km south of the study area. Relocations on 12 July, and 13-14 August were also in this area.

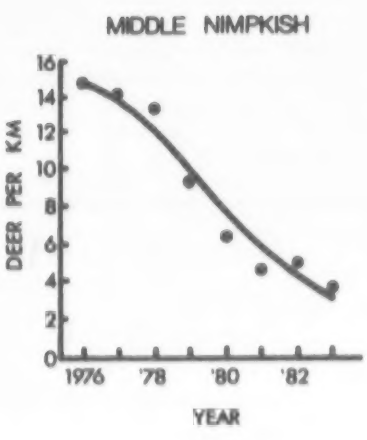
(● Aug-Sep, ■ Oct-Mar, ▲ Apr-May)

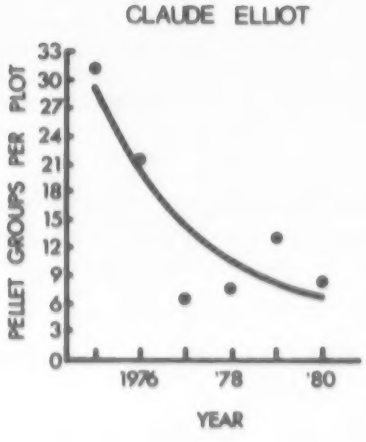


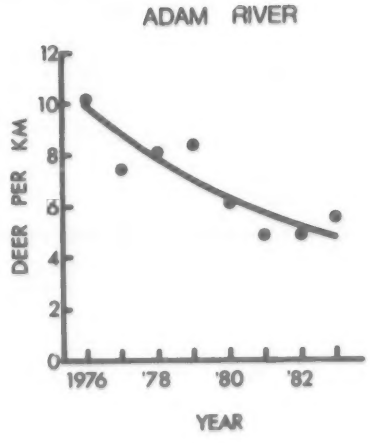
APPENDIX H. Population trends for 4 deer herds on northern Vancouver Island, 1975-83. Each trend was fitted to 10 different model equations: (1) straight line; (2) exponential growth; (3) power function; (4) hyperbolic; (5) exponential saturation: (6) sigmoid: (7) exponential sigmoid; (8) modified inverse; (9) modified power functions; and (10) maxima function (Spain 1982). The equation giving the minimum residual mean square was selected as the most appropriate model. The best equation and related statistical parameters for each population are summarized below:

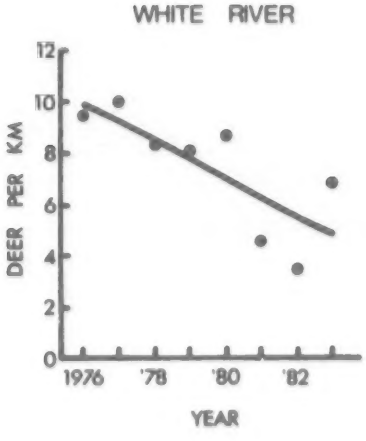
Population	M.U.	Equation	Name	F	Df	Signif. Level
Middle Nimpkish[a]	11-4,5,6,7	$y = \frac{15}{(1+.010x^{2.808})}$	Sigmoid	152	6	$p<.0005$
Claude Elliot[b]	10-16	$y = \frac{40}{(1+.376x^{1.453})}$	Sigmoid	14	4	$p<.025$
Adam River[a]	10-12 13	$y = \frac{11}{(1+.105x^{1.215})}$	Sigmoid	24	6	$p<.005$
White River[a]	10-8	$y = \frac{14}{(1+.325e^{.221x})}$	Exponen. Sigmoid	9	6	$p<.025$

[a] B.C. Fish and Wildlife Branch, Nanaimo
[b] Jones and Mason (1983)









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